FIELDIANA

Geology
NEW SERIES, NO. 20

A Preliminary Survey of Fossil Leaves
and Well-Preserved Reproductive Structures
from the Sentinel Butte Formation (Paleocene)
near Almont, North Dakota

Peter R. Crane

Steven R. Manchester

David L. Dilcher

Information for Contributors to Fieldiana

General: *Fieldiana* is primarily a journal for Field Museum staff members and research associates, although manuscripts from nonaffiliated authors may be considered as space permits.

The Journal carries a page charge of $65.00 per printed page or fraction thereof. Payment of at least 50% of page charges qualifies a paper for expedited processing, which reduces the publication time. Contributions from staff, research associates, and invited authors will be considered for publication regardless of ability to pay page charges, however, the full charge is mandatory for nonaffiliated authors of unsolicited manuscripts. Three complete copies of the text (including title page and abstract) and of the illustrations should be submitted (one original copy plus two review copies which may be machine-copies). No manuscripts will be considered for publication or submitted to reviewers before all materials are complete and in the hands of the Scientific Editor.

Manuscripts should be submitted to Scientific Editor, *Fieldiana*, Field Museum of Natural History, Chicago, Illinois 60605-2496, USA.

Text: Manuscripts must be typewritten double-spaced on standard-weight, 8½- by 11-inch paper with wide margins on all four sides. If typed on an IBM-compatible computer using MS-DOS, also submit text on 5¼-inch diskette (WordPerfect 4.1, 4.2, or 5.0, MultiMate, Displaywrite 2, 3 & 4, Wang PC, Samna, Microsoft Word, Volkswriter, or WordStar programs or ASCII).

For papers over 100 manuscript pages, authors are requested to submit a "Table of Contents," a "List of Illustrations," and a "List of Tables" immediately following title page. In most cases, the text should be preceded by an "Abstract" and should conclude with "Acknowledgments" (if any) and "Literature Cited."

All measurements should be in the metric system (periods are not used after abbreviated measurements). The format and style of headings should follow that of recent issues of *Fieldiana*.

For more detailed style information, see *The Chicago Manual of Style* (13th ed.), published by The University of Chicago Press, and also recent issues of *Fieldiana*.

References: In "Literature Cited," book and journal titles should be given in full. Where abbreviations are desirable (e.g., in citation of synonymies), authors *consistently* should follow *Botanico-Periodicum-Huntianum* and *TL-2 Taxonomic Literature* by F. A. Stafleu & R. S. Cowan (1976 *et seq.*) (botanical papers) or *Serial Sources for the Biosis Data Base* (1983) published by the BioSciences Information Service. Names of botanical authors should follow the "Draft Index of Author Abbreviations, Royal Botanic Gardens, Kew," 1984 edition, or *TL-2*.

References should be typed in the following form:

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, Calif., 943 pp.

Grubb, P. J., J. R. Lloyd, and T. D. Pennington. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. Journal of Ecology, **51:** 567-601.

Langdon, E. J. M. 1979. Yage among the Siona: Cultural patterns in visions, pp. 63-80. *In* Browman, D. L.,and R. A. Schwarz, eds., Spirits, Shamans, and Stars. Mouton Publishers, The Hague, Netherlands.

Murra, J. 1946. The historic tribes of Ecuador, pp. 785-821. <u>In</u> Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

Stolze, R. G. 1981. Ferns and fern allies of Guatemala. Part II. Polypodiaceae. Fieldiana: Botany, n.s., **6:** 1-522.

Illustrations: Illustrations are referred to as "figures" in the text (not as "plates"). Figures must be accompanied by some indication of scale, normally a reference bar. Statements in figure captions alone, such as "× 0.8," are not acceptable. Captions should be typed double-spaced and consecutively. See recent issues of *Fieldiana* for details of style.

All illustrations should be marked on the reverse with author's name, figure number(s), and "top."

Figures as submitted should, whenever practicable, be 8½ × 11 inches (22 × 28 cm), and may not exceed 11½ × 16½ inches (30 × 42 cm). Illustrations should be mounted on boards in the arrangement to be obtained in the printed work. This original set should be suitable for transmission to the printer as follows: Pen and ink drawings may be originals (preferred) or photostats; shaded drawings must be originals, but within the size limitation; and photostats must be high-quality, glossy, black-and-white prints. Original illustrations will be returned to the corresponding author upon publication unless otherwise specified.

Authors who wish to publish figures that require costly special paper or color reproduction must make prior arrangements with the Scientific Editor.

Page Proofs: *Fieldiana* employs a two-step correction system. The corresponding author will normally receive a copy of the edited manuscript on which deletions, additions, and changes can be made and queries answered. Only one set of page proofs will be sent. All desired corrections of type must be made on the single set of page proofs. Changes in page proofs (as opposed to corrections) are very expensive. Author-generated changes in page proofs can only be made if the author agrees in advance to pay for them.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

FIELDIANA

Geology

A Preliminary Survey of Fossil Leaves and Well-Preserved Reproductive Structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota

Peter R. Crane

Department of Geology
Field Museum of Natural History
Chicago, Illinois 60605-2496

Steven R. Manchester and David L. Dilcher

Departments of Geology and Biology
Indiana University
Bloomington, Indiana 47405

Present address:

Department of Botany and Florida Museum of Natural History
University of Florida
Gainesville, Florida 32611-2035

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

Table of Contents

List of Illustrations

List of Tables

A Preliminary Survey of Fossil Leaves and Well-Preserved Plant Reproductive Structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota

Abstract

An unusually well-preserved and diverse Upper Paleocene flora is described from the Sentinel Butte Formation near Almont in central North Dakota. The flora contains approximately 30–45 "biological species" represented by leaves, stems, and a variety of reproductive structures including infructescences, fruits, seeds, staminate inflorescences, and pollen. Angiosperms are dominant in the flora; no pteridophytes and only two species of gymnosperm have been recognized. Specimens are partially compressed and permineralized with silica. Thin sections and scanning electron microscopy of fracture surfaces yield details of anatomical structures and pollen grains. The flora includes fossil taxa that are widespread in other middle and high latitude Paleocene plant assemblages from the Northern Hemisphere, such as *Ginkgo adiantoides,* Taxodiaceae, *Nordenskioldia borealis, Platanus, Palaeocarpinus,* and *Porosia verrucosa*; the exceptional preservation of the Almont material significantly adds to current knowledge of some of these plants. The assemblage also contains many taxa that are unknown in other Paleocene floras. The quality of preservation and the abundance of reproductive structures demonstrated in this preliminary survey suggests that continued work on the Almont flora will clarify the phylogenetic relationships of many Paleocene fossil plants and thus enhance our understanding of the historical development of Recent plant families and communities.

Introduction

The abundant Paleocene megafossil floras of western North America (Berry, 1935; Bell, 1949; Brown, 1962; Chandrasekharam, 1974; Hickey, 1977), along with those of Greenland (Heer, 1869; Seward & Edwards, 1941; Koch, 1963), Spitzbergen (Schloemer-Jäger, 1958; Manum, 1962), Arctic Canada (West et al., 1981), Europe (Forbes, 1851; Saporta, 1868; Gardner, 1887; Laurent, 1912; Johnson, 1937; Seward, 1939; Chandler, 1961; Crane, 1978, 1981a,b; Collinson, 1986; Mai, 1987), central and eastern Asia (Kryshtofovich, 1958; Krassilov, 1976), and Alaska (Hollick, 1936; Wolfe, 1966, 1977) have been the subject of paleobotanical investigation for well over a century. The evidence now available identifies the Paleocene as a critical interval in the diversification of extant flowering plants, and in the early development of Recent plant communities (Muller, 1981; Wolfe & Upchurch, 1986; Crane, 1987; Upchurch & Wolfe, 1987). Late Cretaceous and Early Tertiary faunal changes, particularly the radiation of mammals (Tiffney, 1984; Collinson & Hooker, 1987; Wing & Tiffney, 1987a,b) and major groups of pollinating insects (Crepet & Friis, 1987), also suggest that the Paleocene was an important interval in the development of the specialized pollination syndromes (Crepet, 1984; Crepet & Friis, 1987; Friis & Crepet, 1987) and dispersal mechanisms (Tiffney, 1984) that characterize many extant flowering plants.

During the Paleocene, vegetation at middle and high paleolatitudes in the Northern Hemisphere is represented by numerous fossil floras that are dominated by a small number of relatively widespread taxa. However, knowledge of these plants is based mainly on isolated leaves and pollen, and although flower and fruiting material is occasionally present, it is usually poorly preserved. These problems of preservation have hindered detailed comparisons of Paleocene fossil plants with their living relatives. In this paper we provide a preliminary review of an exceptional and unusually well-preserved Paleocene flora from near Almont, North
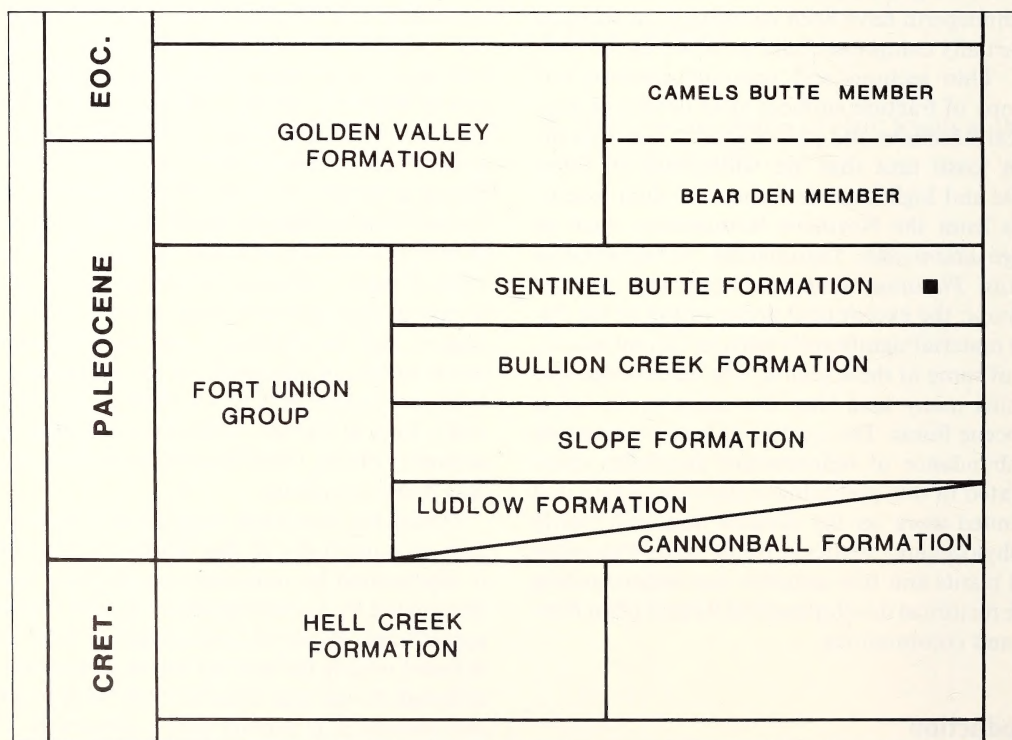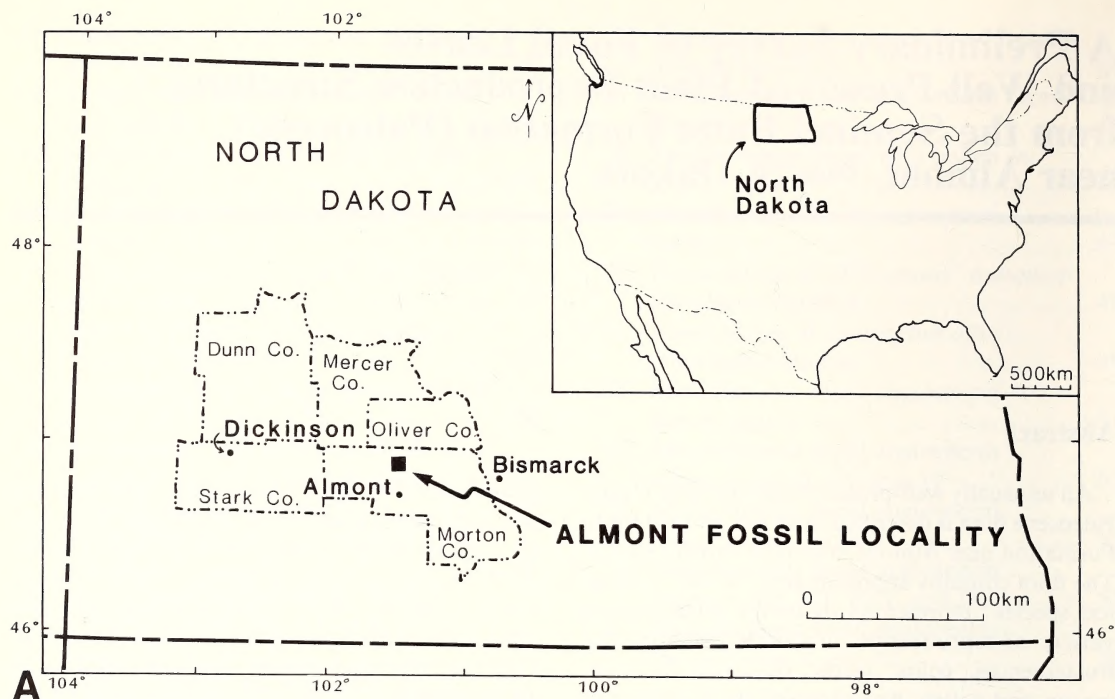
FIG. 1. Geographic and stratigraphic position of the Almont plant fossil locality. **A,** Location of the Almont fossil locality in Morton County, North Dakota. **B,** Generalized stratigraphy of Upper Cretaceous and Lower Tertiary sediments in the Williston Basin (after Lerud, 1982): black square indicates the stratigraphic level of the Almont locality.

Dakota, USA (fig. 1A). Vegetative remains and abundant reproductive structures occur together at the locality, and excellent morphological and anatomical details are preserved. Using evidence of co-occurrence at Almont and at other localities, combined with the systematic relationships of the isolated organs, it is possible to begin to identify the corresponding vegetative and reproductive parts of single species. The Almont flora thus provides an unusual opportunity to understand the structure of Paleocene plants and facilitates detailed systematic comparisons with Recent taxa. The plant assemblage includes some of the earliest representatives of several angiosperm families, and because the flora is from a single locality, it provides new information on ecological associations that is useful in understanding the historical development of Recent plant communities.

Materials and Methods

The fossil plants occur in rocks mapped as part of the Sentinel Butte Formation of the Fort Union Group (Bluemle, 1983) 13 miles north of Almont, Morton County, North Dakota (IU loc. 15722: SE¼ SW¼ Sec. 23, T140N, R86W). The Sentinel Butte Formation is overlain by the Bear Den Member of the Golden Valley Formation (late Paleocene, Hickey, 1977) and is regarded as of late Paleocene age (fig. 1; Clarkforkian, Lerud, 1982). Tiffanian mammals from the underlying sediments in this area of North Dakota (lower Tongue River Formation *sensu* Holtzman, 1978) also indicate a late Paleocene age. The only previously described plants from this locality are fruits and associated leaflets and pollen of *Cyclocarya brownii* (Juglandaceae; Manchester & Dilcher, 1982; Manchester, 1987). The fossils are preserved in a hard, siliceous, iron-stained, yellow-brown, fine-grained shale, which caps a slight rise on the margin of agricultural land. There is no well-exposed geological section, and the shale occurs directly below the topsoil. The plant-bearing layer does not exceed 50 cm in thickness but extends laterally for at least several hundred meters. It directly overlies an unconsolidated fine green-gray sand, and is extensively fractured and penetrated by modern roots throughout its thickness. Fine laminations can be detected in some of the blocks. Fish scales, occasional more complete fish material, and rare insect remains are the only animal fossils known from the locality. The fine laminations, grain size, presence of fish scales, and the limited thickness of the plant bed suggest

that the sediments were deposited in a small fresh-water lake or pond.

Superficial deposits of calcium carbonate and other minerals commonly obscure details of exposed plant fossils but may be removed with concentrated hydrochloric acid. Careful application of the acid often significantly enhances contrast between the fossil and the matrix, and does not appear to affect the quality of preservation of already oxidized specimens. Although the shale is typically oxidized to a yellow-brown color, the center of large blocks is frequently black to dark green-gray and preserves organic material.

The matrix is silica-rich with a tendency to fracture conchoidally. However, large sheets can be collected that show leaves, fruits, stems, and other plant organs on the exposed surfaces. Fruits, stems, and other three-dimensional plant organs are preserved in white to transparent silica. They are little compressed, and preparation of thin sections or scanning electron microscopy of fracture surfaces often reveals excellent anatomical details. Frequently it is useful to glue counterparts of fruits and other structures together with epoxy after they have been examined and photographed on bedding planes. The reassembled specimen can then be sectioned and its three-dimensional structure and anatomical details observed. Pollen grains may be extracted from the matrix using standard paleopalynological preparation techniques. Pollen within silicified anthers of staminate catkins is peculiarly preserved as minute molds and casts with the sporopollenin wall missing. The occurrence of morphologically preserved leaves, infructescences, and other organs in the same deposit as anatomically preserved shoots, wood, fruits, and seeds makes the Almont flora unique in the range of botanical details that can be studied from a single Paleocene locality.

Large collections of the Almont flora have been made since 1982 and are housed in the Florida Museum of Natural History (formerly collections of the Departments of Geology and Biology, Indiana University [IU]), and the Department of Geology, Field Museum of Natural History (PP). These two collections, in addition to those of the University of North Dakota, Grand Forks, North Dakota (UND), have provided the material described in this paper. The combined Field Museum and Florida Museum collections from the Almont locality now include more than 2,000 specimens. The relative abundance of each fossil entity within these collections is indicated in Table 1 (p. 4).

Details of other localities in the Paleocene of

TABLE 1.   Relative abundance of plant fossils at the Almont locality. Abundances are based on numerical estimates of specimens of each taxon in the paleobotanical collections of the Field Museum of Natural History and Florida Museum of Natural History. Total number of specimens is approximately 2,000. Relative abundance is estimated using a six-point logarithmic scale modified from Spicer and Hill (1979).

Taxon or structure	Organ	Relative abundance*
Ginkgoaceae	Leaves	Very common
Ginkgo adiantoides (Unger) Heer	Seeds	Common
Taxodiaceae	Leafy shoots	Common
cf. *Parataxodium* Arnold & Lowther	Ovulate cones	Occasional
	Pollen cones	Common
	Seeds	Rare
Menispermaceae		
cf. *Canticocculus* Chandler	Fruits	Very rare
Trochodendraceae	Fruits	Occasional
Nordenskioldia borealis Heer	Dispersed achenes	Very common
	Leaves	Abundant
Cercidiphyllaceae	Follicles	Rare
Nyssidium arcticum (Heer) Iljinskaja	Leaves	Very rare
	Staminate inflorescences	Very rare
Platanaceae	Leaf type A	Rare
	Leaf type B	Rare
	Leaf type C	Very rare
	Staminate inflorescences	Very rare
Hamamelidaceae	Infructescences	Occasional
Betulaceae	Infructescences + fruits	Abundant
Palaeocarpinus sp.	Staminate inflorescences	Common
	Leaves	Abundant
Juglandaceae	Fruits	Abundant
Cyclocarya brownii Manchester & Dilcher	Leaves	Occasional
Myrtaceae		
?*Psidium*	Fruits + seeds	Occasional
Cornaceae		
Cornus sp.		Rare
Meliosmaceae		
Meliosma rostellata (Lesquereux), comb. nov.	Fruits	Occasional
Icacinaceae		
Palaeophytocrene sp.	Fruits	Very rare
Miscellaneous fossil angiosperm reproductive structures		
Schizocarpic samara	Fruits	Very common
Nonschizocarpic samara	Fruits	Occasional
Elliptical biwinged fruit		Very rare
Fruit with three laterally attached wings		Very common
Pedicellate capsule with papillate seeds		Rare
Head of tricarpellate fruits	Heads	Occasional
	Individual fruits	Very common
Six- to seven-loculed fibrous fruit		Very common
Fruit of 9 to 11 single-seeded locules		Very rare
Thick-walled unilocular fruit		Very common
Globose fruit with irregular surface pits		Rare
Six-lobed calyx		Very rare
Fruit with five to six concrescent follicles		Rare
Clavate structure		Rare
Fleshy fruit		Rare
Four-loculed winged fruit		Very rare
Globose pedicellate capsule		Rare
Asymmetric ellipsoidal seed		Very rare
Elongate infructescence		Rare
Staminate inflorescence with tricolpate pollen		Rare
Staminate inflorescence with monosulcate pollen		Very rare
Miscellaneous fossil angiosperm leaves		
Monocotyledonous leaf fragments		Very rare
Porosia verrucosa (Lesquereux) Hickey		Occasional

TABLE 1. Continued.

Taxon or structure	Organ	Relative abundance*
Lacunate leaf		Very rare
"*Viburnum*" *antiquum* (Newberry) Hollick		Common
Averrhoites affinis (Newberry) Hickey		Rare
Leaf type I		Occasional
Leaf type II		Very rare
Leaf type III		Very rare
Leaf type IV		Very rare
Leaf type V		Very rare
Leaf type VI		Very rare
Leaf type VII		Very rare
Leaf type VIII		Rare
Leaf type IX		Rare
Leaf type X		Very rare
Leaf type XI		Very rare

* Abundant (>120), Very common (60–119), Common (30–59), Occasional (16–29), Rare (6–15), Very rare (1–5).

North America, which are mentioned in the text, are as follows: USGS 8519, "hillside south of U.S. Highway 10, 25 miles east of Miles City, Mont." (Brown, 1962, p. 33); USGS 9109, "NW¼ SW¼ sect. 29, T1S, R6E, 13 miles east of Riverton, Wyo." (Brown, 1962, p. 34); USGS 9438, "Monument Hills District, Wyoming"; IU loc. 15740, SW¼, Sec. 7, T35N, R85W, Hell's Half Acre, Wyoming; IU loc. 15757, Centr. Sec. 17, T34N, R92W, Signor Ridge, Wyoming; IU loc. 15778, Just N of Centr. Sec. 26, T16N, R102W, Big Flat Draw, Wyoming.

In this paper we provide brief preliminary descriptions and comparisons of the different plant fossils that have been recognized, along with a short discussion of their significance. In most instances associated organs thought to have been produced by the same taxon are treated together under a single generic or specific name, but this does not imply assignment of the different organs to a single nomenclatural entity. Fossil organs that can be confidently assigned to an extant angiosperm family are treated in sequence broadly according to the classification of Cronquist (1981). This is followed by consideration of miscellaneous angiosperm fruits and seeds, and then miscellaneous angiosperm leaves. More detailed accounts of selected taxa are in preparation.

Descriptions and Discussion of Plant Fossils

Ginkgoaceae

Ginkgo adiantoides (Unger) Heer.
Figure 2A,B,D–G.

Leaves are 4–15 cm wide and up to 15 cm long, excluding the petiole, which may be up to 6 cm long (fig. 2A). Seeds are up to 2 cm long when the sarcotesta is preserved (fig. 2D,E). The sclerotesta is 8–15 mm long, 9–12 mm wide, and is bilaterally symmetrical with the major plane of symmetry marked by a prominent keel (fig. 2F). Seed-bearing stalks are up to 9 cm long with two ovules at the apex (fig. 2B,G). All of our specimens are stalks from which one mature seed had abscissed, leaving a broad attachment scar alongside the remains of an aborted ovule and collar (fig. 2G).

Fossil leaves of *Ginkgo* are widely distributed in the Early Tertiary of the Northern Hemisphere (Tralau, 1968) and, in macroscopic characters, leaves of *Ginkgo adiantoides* cannot be distinguished from those of extant *G. biloba* L., the only living representative of the Ginkgoaceae. Knowledge of Early Tertiary *Ginkgo* is based solely on leaves, and casts or molds of the seed sclerotesta. The specimens from Almont expand the information available, and show that the seeds in Early Tertiary *Ginkgo* were borne exactly as in the extant species (fig. 2C,H; see Prynada, 1962, for comparable seed-bearing stalks from the Middle Jurassic of the USSR). This supports the concept of *Ginkgo* as a classic example of stasis in the plant fossil record. The only differences recognized so far between the Early Tertiary species and extant *G. biloba* are in seed size, minor features of cuticle morphology, and wood anatomy (Florin, 1936; Manum, 1966; Mastroguiseppe et al., 1970). The seeds associated with *G. adiantoides* at Almont are approximately twice the size of those associated with *Ginkgo huttoni* (Sternberg) Heer in the Jurassic of Yorkshire (Harris et al., 1974), and
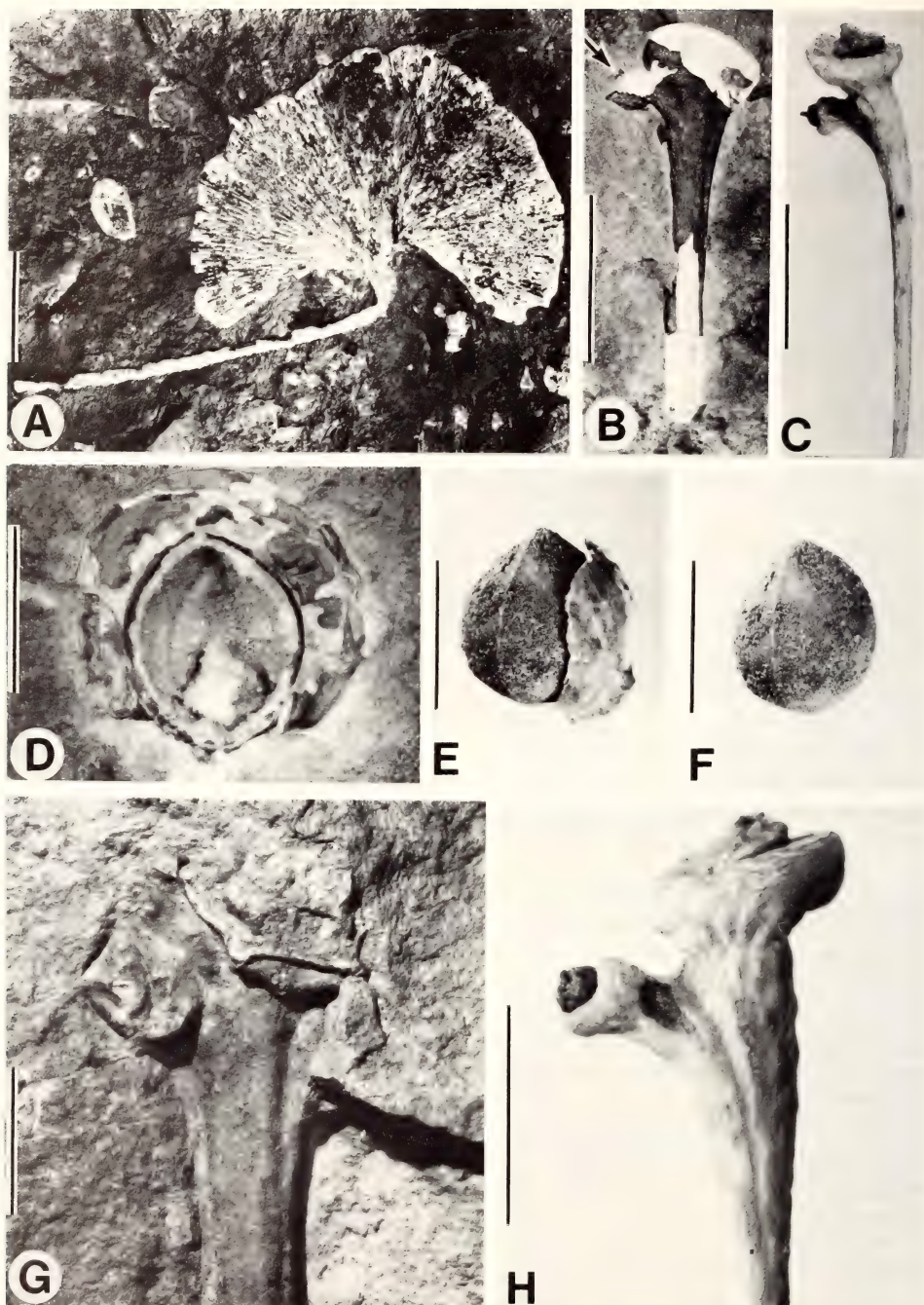
FIG. 2.   Fossil and extant *Ginkgo* (Ginkgoaceae). **A,** *Ginkgo adiantoides* (Unger) Heer, fossil leaf, UND 13055, ×0.75. **B,** *Ginkgo* fossil ovule stalk showing an aborted ovule (arrow) and expanded apex where a mature seed was attached, IU 5966, ×2.3. **C,** Extant *Ginkgo biloba* L., apex of ovule stalk; cf. B, ×2. **D,** *Ginkgo* fossil seed; longitudinal fracture showing remains of fleshy sarcotesta surrounding the sclerotesta, PP34195, ×2.3. **E,** *Ginkgo* fossil seed removed from matrix showing exterior of sclerotesta and adhering fragment of sarcotesta, IU 5967, ×2. **F,** Seed in E with sarcotesta removed to show the bilaterally symmetrical sclerotesta, ×2. **G,** *Ginkgo* fossil ovule stalk showing detail of aborted ovule, collar (left) and the area where a mature seed was attached (right), PP34187, ×4. **H,** Extant *Ginkgo biloba* L., detail of apex of ovule stalk showing aborted ovule and expanded apex where a mature seed was attached, ×6. Scale bars: A, 2 cm; B–F, 1 cm; G, H, 5 mm.

approximately half the size of the seeds of extant *G. biloba.*

Taxodiaceae

cf. ***Parataxodium*** Arnold & Lowther.
Figures 3 and 4.

Leafy shoots vary considerably in morphology with leaves ranging from linear to scale-like (fig. 3A–D). Linear leaves are 8–30 mm long and 1–3 mm wide, with the angle of attachment to the stem about 30–80°. Linear leaves are abruptly contracted at the base and usually acute (rarely rounded) at the apex. They have a prominent midrib, and epidermal cells with distinctly sinuous periclinal walls (fig. 3F). Linear leaves are attached both helically, and in opposite and decussate pairs. Scale leaves are acicular and typically 2–3 mm long (fig. 3D). Several specimens demonstrate that linear leaves and scale leaves were borne on the same shoot systems (e.g., fig. 3C).

Associated seed cones are apical on a stalk up to 6 cm long. The cone stalk is naked except for a few scattered scales. Cones vary from almost circular to elliptic in outline and are 2–3 cm in diameter. Each consists of about 30–40 woody scales that have an expanded head and a narrow stalk. None of our specimens show the outer surface of the cone, and we are therefore uncertain whether the cone scales are helically arranged or in opposite and decussate pairs. Cones are anatomically preserved and thin sections show the distribution of vascular tissue as well as occasional seeds. The seeds are difficult to recognize in fractures through the cones, but are occasionally found dispersed (fig. 3G,H).

Associated pollen cones (fig. 4A–E) are borne on specialized shoots typically 4–5 cm long, with 15–25 cones in the axils of short narrow bracts. The cones are borne in opposite and decussate pairs except at the shoot apex. Each cone is circular or slightly ellipsoidal in outline and consists of numerous overlapping scales (fig. 4C). Details of cone morphology have not been investigated, but thin sections reveal masses of *in situ* pollen (fig. 4F,G). Pollen grains are inaperturate and occasionally show a germinal papilla (fig. 4G).

The morphology of the shoots, pollen, and seed cones is similar to that in the extant family Taxodiaceae (tribe Cupresseae of the Cupressaceae, *sensu* Eckenwalder, 1976), particularly the five

closely related genera *Glyptostrobus, Metasequoia, Sequoia, Sequoiadendron,* and *Taxodium.* Although only one species of seed cone and one species of pollen cone are present at the Almont locality it is uncertain whether there are one or two species of taxodiaceous foliage. While several of the shoots show opposite phyllotaxy as in *Metasequoia,* in many specimens the phyllotactic pattern is unclear. In addition, although these linear leaves have epidermal cells with undulate anticlinal walls (fig. 3F), which are diagnostic of *Metasequoia* among extant Taxodiaceae (Chaney, 1951; Basinger, 1981, 1984), the leaf apex is more acute and the angle of leaf divergence is less than in the extant genus (Arnold & Lowther, 1955). Shoots with scale leaves do not occur in extant *Metasequoia,* and the fossil shoots of this type are similar to those of *Glyptostrobus.* A few of these specimens show the transition from scale leaves to linear leaves (fig. 3C), but it has not been possible to show the transition from helical to opposite phyllotaxy necessary to demonstrate that the *Glyptostrobus*-type and *Metasequoia*-type foliage was produced by a single fossil taxon.

The seed cones from Almont differ from those of *Glyptostrobus* in having peltate rather than imbricate scales, and although the exact arrangement of cone scales is not known, the absence of well-developed leaves on the cone stalk is a unique characteristic of *Metasequoia* among extant Taxodiaceae. The pollen cones are also similar to those of *Metasequoia.*

Brown (1962) recognized three taxodiaceous conifers in the Fort Union Formation of western North America, *Glyptostrobus nordenskioldi* (Heer) Brown, *Metasequoia occidentalis* (Newberry) Chaney, and *Taxodium olriki* (Heer) Brown. Permineralized material of *M. occidentalis* has been reported from the Paleocene of North Dakota by Harr and Ting (1976). Our material differs from extant *M. glyptostroboides* Hu & Cheng, fossil *M. occidentalis,* as well as the anatomically preserved Middle Eocene species *M. milleri* (Rothwell & Basinger, 1979; Basinger, 1981, 1984) in phyllotaxy and in the presence of scale leaves. The foliage of the Almont species is most similar to that of *T. olriki,* but cones of this species have not been described (Brown, 1962), and this precludes more detailed comparison with our material. The genus *Parataxodium* was named by Arnold and Lowther (1955) to accommodate taxodiaceous leaves and cones from the Late Cretaceous of Alaska, which principally differed from *Metasequoia* in having an alternate rather than opposite arrangement of
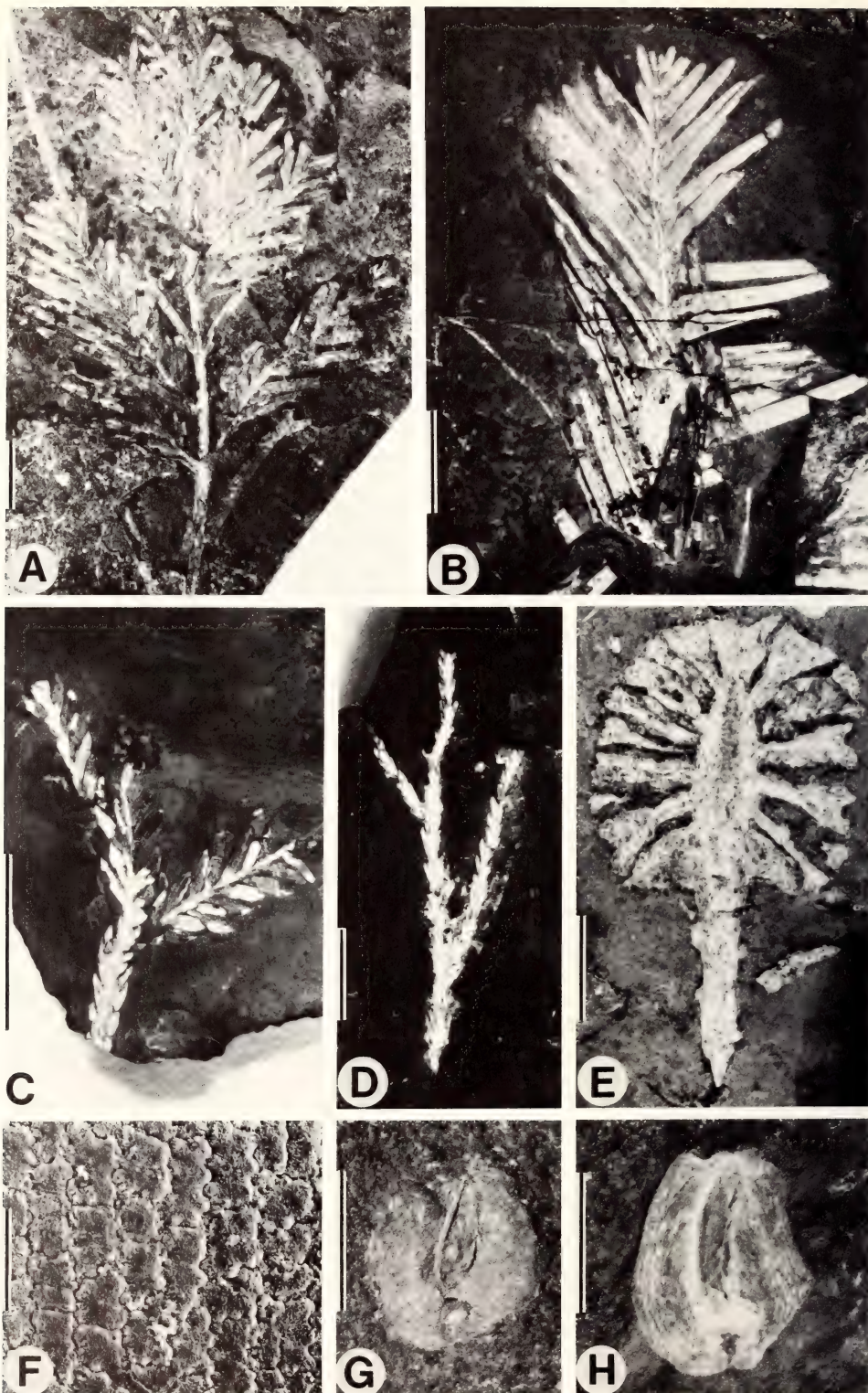
Fɪɢ. 3. Fossil leafy shoots, ovulate cone, and seeds of Taxodiaceae, cf. *Parataxodium* Arnold & Lowther. **A,** Terminal shoot system with linear leaves, ᴜɴᴅ 13056, ×1. **B,** Leafy shoot with linear leaves, ᴘᴘ34186, ×1.5. **C,** Leafy shoot showing acicular scale-leaves proximally, and linear leaves distally, ᴘᴘ34196, ×2.5. **D,** Shoot with acicular scale-
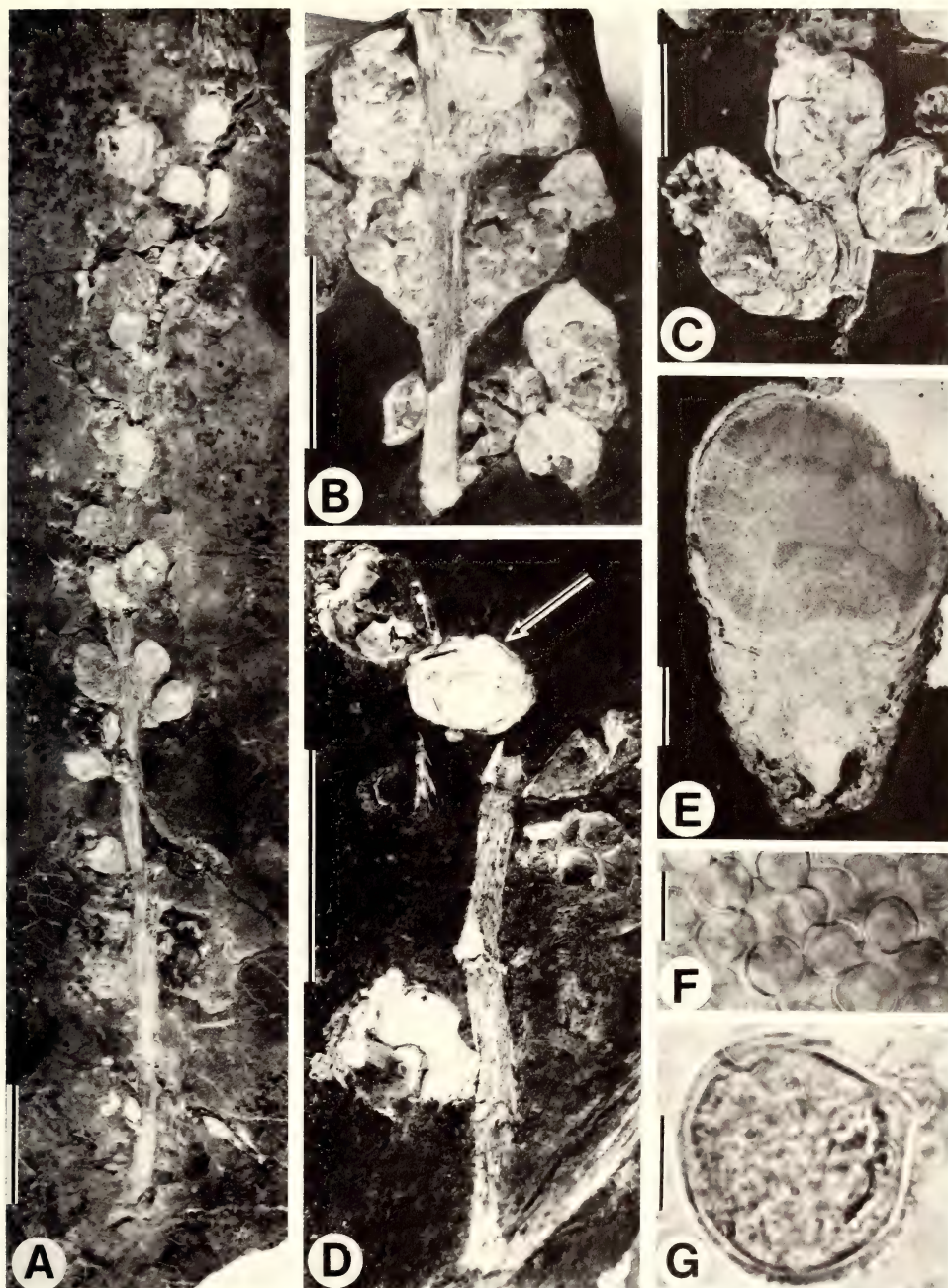
FIG. 4. Fossil pollen cones of Taxodiaceae, cf. *Parataxodium* Arnold & Lowther. **A,** Long axis with numerous attached pollen cones, IU 5980, ×1.5. **B,** Portion of axis showing opposite arrangement of pollen cones, IU 6173, × 2.5. **C,** Terminal portion of cone-bearing axis, IU 6172, ×3. **D,** Cone-bearing axis and three cones; arrow indicates cone sectioned in E, IU 6174, ×3. **E,** Longitudinal thin section through the cone in D, ×10. **F,** Inaperturate pollen grains *in situ* within the cone in E, ×300. **G,** Pollen grain from E showing germinal papilla, ×1,200. Scale bars: A, B, D, 1 cm; C, 5 mm; E, 1 mm; F, 30 μm; G, 10 μm.

←
leaves, PP34007, ×1.25. **E,** Longitudinal fracture through ovulate cone showing peltate cone scales, PP33948, ×1.5. **F,** Scanning electron micrograph of silica replaced leaf fragment showing files of epidermal cells with sinuous walls, PP34194, ×300. **G,** Dispersed seed showing seed body, wing, apical micropyle, and basal notch, IU 6271, ×4. **H,** Dispersed seed showing seed body, wing, apical micropyle, and basal notch, IU 6272, ×4. Scale bars: A–E, 1 cm; F, 50 μm; G, H, 5 mm.
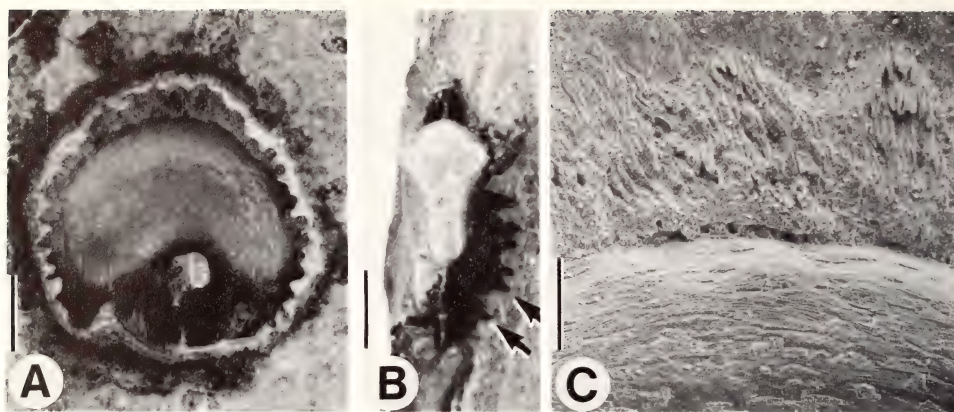
Fɪɢ. 5. Fossil fruit of the Menispermaceae, cf. *Canticocculus* Chandler, ɪᴜ 6264. **A,** Lateral fracture plane showing the outline of the ribbed endocarp and the reniform locule-cast, ×10. **B,** Transverse section perpendicular to the fracture plane in A, showing pear-shaped outline of the locule-cast and sections through the ribs on the endocarp (arrows), ×10. **C,** Scanning electron micrograph of the fracture plane in A showing longitudinal striations on the surface of the locule-cast and cellular details of the endocarp, ×60. Scale bars: A, B, 1 mm; C, 200 μm.

leaves on the shoots. Until a more detailed study of the Almont species is carried out we provisionally assign our material to *Parataxodium*. *Parataxodium* has also been recorded from the uppermost Cretaceous or lowermost Paleocene of Spitzbergen (Schweitzer, 1974) and Sakhalin (Krassilov, 1978).

Menispermaceae·

cf. ***Canticocculus*** Chandler. Figure 5.

Endocarp is fibrous, C-shaped, and 3 mm high, 2.5 mm broad, and 1.5 mm deep. The endocarp surface is ribbed. The locule-cast is reniform with a smooth surface.

When initially exposed, the specimen illustrated in Figure 5A was seen in lateral section, showing the general outline of the locule-cast and fibrous endocarp (fig. 5C). It was subsequently sectioned transversely through the curved long axis to show the pear-shaped outline of the locule and the ribs on the surrounding endocarp (fig. 5B). The C-shaped configuration of the endocarp and locule combined with the pear-shaped cross section of the locule is closely similar to endocarps of the tribe Cocculeae in the Menispermaceae (Thanikaimoni, 1984). Similar material has been described from the Lower Eocene London Clay flora from southern England as *Canticocculus cooperi* Chandler (1961; Collinson, 1983) and from the Upper Paleocene of Gonna-Walkmühle, near Sangerhausen, DDR, as *Cocculus cooperi* (Chandler)

Mai (1987). Mai (1987) acknowledges the differences between this fossil material and the extant genus, but he reduced *Canticocculus* to sectional level, regarding the differences as insufficient for the recognition of an extinct genus. Although our material conforms to the diagnosis, it differs from *C. cooperi* in having shorter limbs to the endocarp. The specimens from Almont are significant as one of the earliest known records of the Cocculeae, and we are not aware of specimens from any other Paleocene localities in North America. Possible leaves of Menispermaceae are very rare at the Almont locality and are described as leaf type X (p. 56, fig. 36A,B).

Trochodendraceae

Nordenskioldia borealis Heer. Figures 6–9.

Infructescences consisting of long, woody axes bearing irregularly spaced schizocarp-like fruits, each formed from a whorl of approximately 15 radially arranged achene-like fruitlets (nutlets; figs. 6A, 7A). The most complete infructescence from Almont shows fruits borne along an infructescence axis 7 cm long. Fruitlets are wedge-shaped in transverse section (fig. 6C,D) and semi-elliptical in outline (fig. 6G,H). Each fruit is approximately 12–15 mm in diameter, 8–10 mm high, sessile on the infructescence axis, and is partially embedded in a shallow cup-like receptacle. This receptacle and the central column, around which the fruitlets are arranged, remain attached to the infructes-

cence axis after the fruitlets have been dispersed. A few specimens show scars on the outer surface of this receptacle that may indicate the position of stamens. Perianth parts or other floral organs have not been observed. At the apex the fruit is bilaterally symmetrical with the fruitlets forming two rows (fig. 6B). At the fruit base, the fruitlets are radially arranged. In transverse section each fruitlet is thin at its attachment to the central column and broadens toward the outside where two broad wedges of parenchyma flank the locule (fig. 6D). Typically about six longitudinal ridges of sclerenchyma extend from the base to the apex of the lateral fruitlet walls (fig. 6D,G). The fruitlets usually contain a seed, although seed size varies from carpel to carpel within a single fruit (fig. 6C). Occasionally a locule is empty and the ovule apparently failed to develop. In transverse section the seeds show a narrow wing along each margin (fig. 6D). The outermost cell layer of the seed coat is clearly differentiated, with thick inner periclinal and anticlinal cell walls and thin outer periclinal cell walls. At maturity fruitlets were shed individually (fig. 6G,H). The wedge-like morphology is usually clearly visible in dispersed fruitlets, the straight inner edge being thin, and the curved outer edge being more deeply impressed into the matrix. Where a fracture plane has passed along the achene surface the longitudinal ridges are clearly visible (fig. 6G). They diverge slightly toward the curved margin and occasionally branch. Dispersed fruitlets indicate that the seeds were probably attached toward the inner margin of the locule.

Infructescence axes of *Nordenskioldia* are well preserved (fig. 7), and are unusual in having wood that lacks the vessel elements characteristic of most extant flowering plants (see also Mathiesen, 1932). One-third of the stem diameter is occupied by a central pith of more or less isodiametric cells (fig. 7B,D). The wood is composed almost exclusively of radial files of tracheids separated by occasional uniseriate rays. The tracheids show circular to elliptical bordered pits (fig. 7C). Pits to ray parenchyma are elliptical to scalariform (fig. 7E). Vegetative shoots in the Almont flora (fig. 8) show identical anatomy to the infructescence axes, and are therefore attributed to the *Nordenskioldia* plant. Externally these shoots have prominent lenticels like those on many *Nordenskioldia* infructescence axes. Strongly differentiated short shoots are present and are up to 12 mm long and 5 mm wide (fig. 8A,B). Short shoots are alternately arranged with crowded leaf scars and a small terminal bud (fig. 8A,B).

Leaves of "*Cocculus*" *flabella* (Newberry) Wolfe (1966) are abundant at the Almont locality and they may be related to the *Nordenskioldia* plant (fig. 9). They have a very broadly elliptical to circular lamina typically 2–7 cm long, 2.3–10.0 cm wide, with a length/width ratio of 0.75–1.25. The apex is obtuse, rounded, or sometimes retuse; leaf base is obtuse or decurrent with a long petiole, up to 6 cm long (fig. 9C). The primary venation is actinodromous, with the secondary and tertiary veins forming loops inside the margin (fig. 9B). Fourth and fifth order veins delimit irregular polygonal areolae with freely ending veinlets (fig. 9D). The margin varies from entire to undulate and crenate. The marginal configuration is usually irregular and gland-tipped chloranthoid teeth are rarely present (fig. 9A–C). Leaves of this general type are usually included in the "*Cercidiphyllum arcticum* complex" (Brown, 1939, 1962; Wolfe, 1966; Hickey, 1977) and are associated with *Nordenskioldia* at many localities in the Fort Union Formation and elsewhere in the Northern Hemisphere, ranging in age from Paleocene to Miocene. On the basis of this association evidence it is very likely that these leaves were the foliage of the *Nordenskioldia* plant.

Nordenskioldia borealis fruits were first described from the Paleocene of Spitzbergen (Heer, 1870) and have subsequently been shown to be widespread in middle and high latitude Late Cretaceous and Paleocene plant assemblages from the Northern Hemisphere (Kryshtofovich, 1958; Brown, 1962; Chandrasekharam, 1974; Takhtajan, 1974; Tanai, 1981). They are represented by about 30 specimens in our collections and the silicified preservation permits a more detailed understanding of their structure and systematic relationships. Kryshtofovich (1956, 1958) was the first to suggest a relationship between *Nordenskioldia* and Trochodendraceae based on compressions of the fruits and the associated foliage. The new information on fruits and wood anatomy provided by the Almont material confirms this hypothesis. The extant vesselless angiosperms *Tetracentron* and *Trochodendron* have gynoecia of 4 and 4–11 laterally concrescent carpels, respectively (Bailey & Nast, 1945; Nast & Bailey, 1945; Smith, 1945; Endress, 1986). *Tetracentron* also has inflorescences that consist of long spikes of sessile flowers. However, both extant genera differ from *Nordenskioldia* in having six or more seeds per carpel and possessing multiseriate rays in the secondary xylem. The major venation of leaves associated with *Nordenskioldia* is similar to that

Fig. 6. Fossil fruits and infructescence of *Nordenskioldia borealis* Heer (Trochodendraceae). **A,** Fruiting axis with attached schizocarp-like cluster of achenes (nutlets), PP34512, ×2. **B,** Apical view of a fruit removed from the matrix, PP34535, ×3. **C,** Transverse section through fruit in B, showing radial arrangement of 15 wedge-shaped achenes, each containing a single seed, ×5. **D,** Detail from C showing a single wedge-shaped achene, boundary between adjacent

in *Tetracentron* and *Cercidiphyllum* (see Wolfe, 1966, 1973) but the fossil leaves usually lack the glandular crenations seen in these extant genera. Extant *Cercidiphyllum* resembles *Nordenskioldia* in having uniseriate rays in the secondary xylem, and in fossil *Cercidiphyllum*-like plants the arrangement of vascular bundles in the follicles (fig. 10G; Crane, 1984; Crane & Stockey, 1985) is very similar to that in the dispersed *Nordenskioldia* achenes (Brown, 1962, p. 89). The information currently available indicates that *Nordenskioldia* is closely related to *Tetracentron, Trochodendron,* and *Cercidiphyllum* (see also Crane, 1989) but the precise systematic relationships remain to be clarified.

Cercidiphyllaceae

Nyssidium arcticum (Heer) Iljinskaja.
Figure 10.

Ellipsoidal follicles are typically 2 cm long and 1 cm wide, with a single longitudinal suture (fig. 10G). The mesocarp has numerous slightly oblique longitudinal vascular bundles, and the endocarp is composed of a mass of transverse fibers.

Associated staminate inflorescences consist of triangular bracts up to 1 cm long with rounded apices (fig. 10D,E). Numerous narrowly elliptical anthers 0.7–1.5 mm long are associated with these bracts and were probably borne in their axils (fig. 10F).

Associated leaves (*Trochodendroides arctica* (Heer) Berry) are elliptical to broadly ovate and may be up to 7 cm long and 6 cm wide, with a length/width ratio of 1.0–1.5. The leaf apex is obtuse and the base obtuse to cordate. The leaf margin has regularly arranged, small, gland-tipped crenations supplied by tertiary veins (fig. 10B). The major venation is actinodromous with secondary and tertiary veins forming loops well within the margin. Fine venation is poorly preserved.

The Almont specimens are clearly similar to other previously described fossil material that has been shown to be closely related to extant Cercidiphyllaceae (Crane, 1984; Crane & Stockey, 1985,

1986). The extant genus *Cercidiphyllum* contains two living species that are native to the mixed mesophytic forests of China and Japan (Swamy & Bailey, 1949; Spongberg, 1979). During the early Tertiary, fossil *Cercidiphyllum*-like plants were widespread (Brown, 1939; Schloemer-Jäger, 1958; Krassilov, 1973a, 1976, 1977; Chandrasekharam, 1974; Iljinskaja, 1974; Scott & Wheeler, 1982; Basinger & Dilcher, 1983; Stockey & Crane, 1983; Crane, 1984; Crane & Stockey, 1985, 1986) and were evidently an important component of early successional vegetation (Crane & Stockey, 1985; Crane, 1987). Consequently, at many localities, *Joffrea*-like leaves and infructescences dominate the fossil assemblage, but in the large collections from Almont they are only represented by a few leaves, two isolated follicles, and three staminate inflorescences. Infructescences and the characteristic winged seeds of these fossil *Cercidiphyllum*-like plants have not been recognized.

Infructescences and isolated follicles of fossil *Cercidiphyllum*-like plants are referred to *Nyssidium* while the leaves have been referred to the fossil genus *Trochodendroides* as well as various extant genera (Brown, 1939; Schloemer-Jäger, 1958; Crane, 1984). From the Paleocene of southern Alberta, one of these plants (*Joffrea speirsii* Crane & Stockey) is known from leaves, inflorescences, infructescences, seeds, seedlings, shoots, and possible staminate inflorescences (Stockey & Crane, 1983; Crane & Stockey, 1985). *Joffrea* differs from extant *Cercidiphyllum* in a range of features associated with shoot morphology and pistillate and staminate inflorescences. Shoot and infructescence structure varies considerably in these fossil taxa and indicates that the Cercidiphyllaceae were probably diverse at the species level during the latest Cretaceous and Early Tertiary (Crane & Stockey, 1986). The absence of well-preserved infructescences at Almont precludes detailed comparison with previously described material.

Platanaceae. Figures 11–14.

Three kinds of platanoid leaves and one probable platanaceous staminate inflorescence have

---

← achenes indicated by arrows; note single seed with narrow wing along both margins, ×15. **E,** Tangential longitudinal section through the fruit in A showing thick achene wall and a single seed within each locule; central portion of fruit showing probable insect damage, ×6. **F,** Cellular details of achene margin from D, ×90. **G,** Dispersed achene fractured along outer surface showing lateral ribs and seed outline, PP34210, ×4. **H,** Dispersed achene fractured through the fibrous endocarp. IU 5968, ×4. Scale bars: A, 1 cm; B, C, E, 5 mm; D, 1 mm; F, 100 μm; G, H, 3 mm.
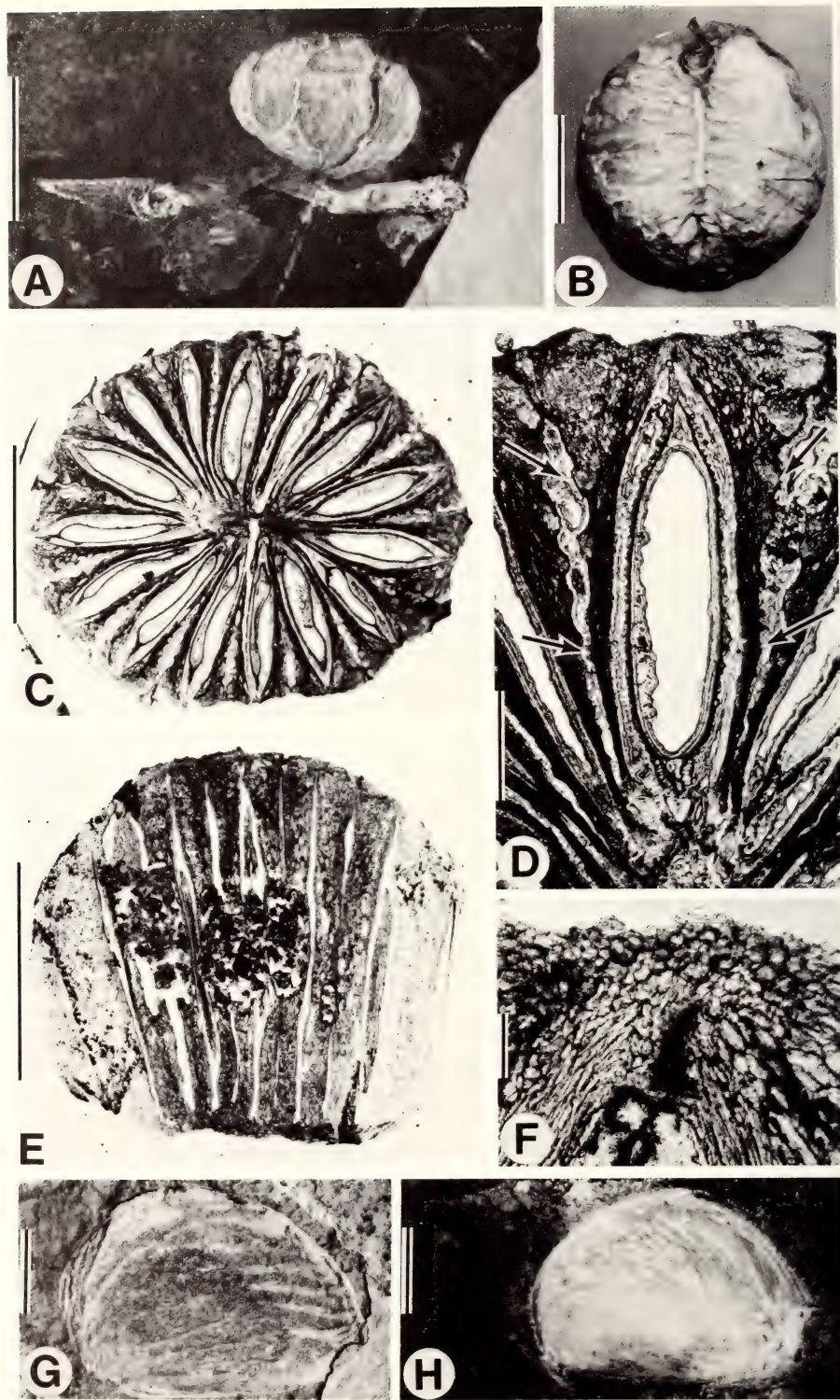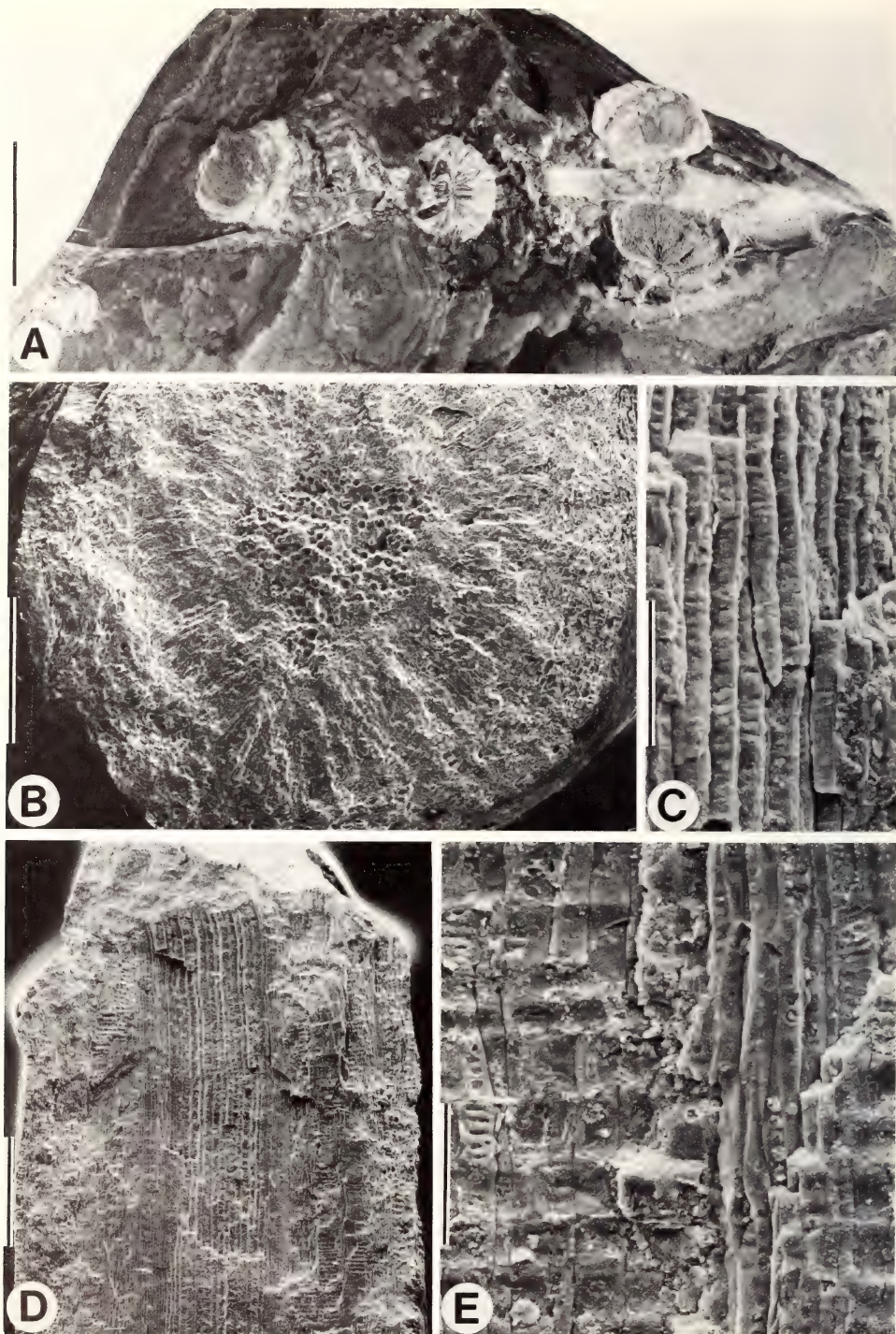
Fɪɢ. 7. Fossil infructesence of *Nordenskioldia borealis* Heer (Trochodendraceae). **A,** Fruiting axis with five attached schizocarp-like clusters of achenes (nutlets), ᴘᴘ34536, ×2. **B,** Scanning electron micrograph of transverse section of fruiting axis from A showing parenchyma forming a central pith surrounded by secondary xylem that lacks vessels, ×40. **C,** Scanning electron micrograph of radial longitudinal section of fruiting axis in A showing tracheids with circular–elliptical pits, ×400. **D,** Scanning electron micrograph of longitudinal section of fruiting axis in A showing large parenchyma cells of pith flanked by tracheids on either side, ×30. **E,** Scanning electron micrograph of radial longitudinal section of fruiting axis in A showing tracheids with circular pits to adjoining tracheids and scalariform pits to adjoining ray cells, ×400. Scale bars: A, 1 cm; B, D, 500 μm; C, E, 50 μm.
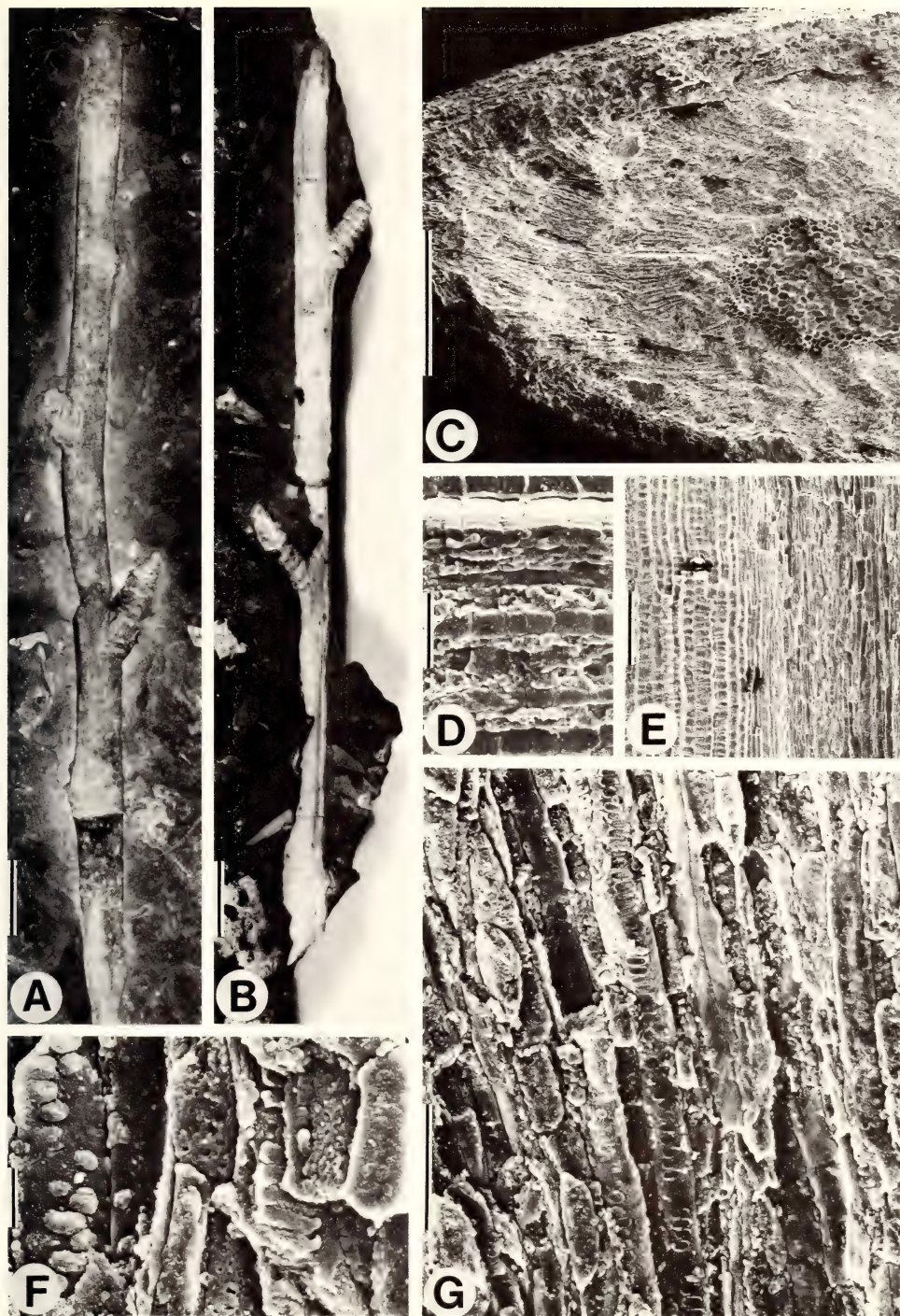
Fig. 8. Probable shoots of *Nordenskioldia borealis* Heer (Trochodendraceae). **A,** Shoot system showing alternately arranged short-shoots, PP34202, ×1. **B,** Shoot system showing alternately arranged short-shoots, PP34207, ×1. **C,** Scanning electron micrograph of transverse section from A showing pith and secondary xylem; cf. *Nordenskioldia* infructescence axis in Figure 7B, ~ ×20. **D,** Detail of transverse section from A showing tracheids and uniseriate rays, ~ ×200. **E,** Detail of radial longitudinal section from A showing vertical files of pith parenchyma (left) and tracheids (right), ×50. **F,** Detail of tracheids in radial longitudinal section from B showing casts of scalariform to circular pits, ×800. **G,** Radial longitudinal section from B showing short parenchyma cells and elongate tracheids with scalariform and circular pits, ×350. Scale bars: A, B, 1 cm; C, 1 mm; D, G, 50 μm; E, 200 μm; F, 10 μm.
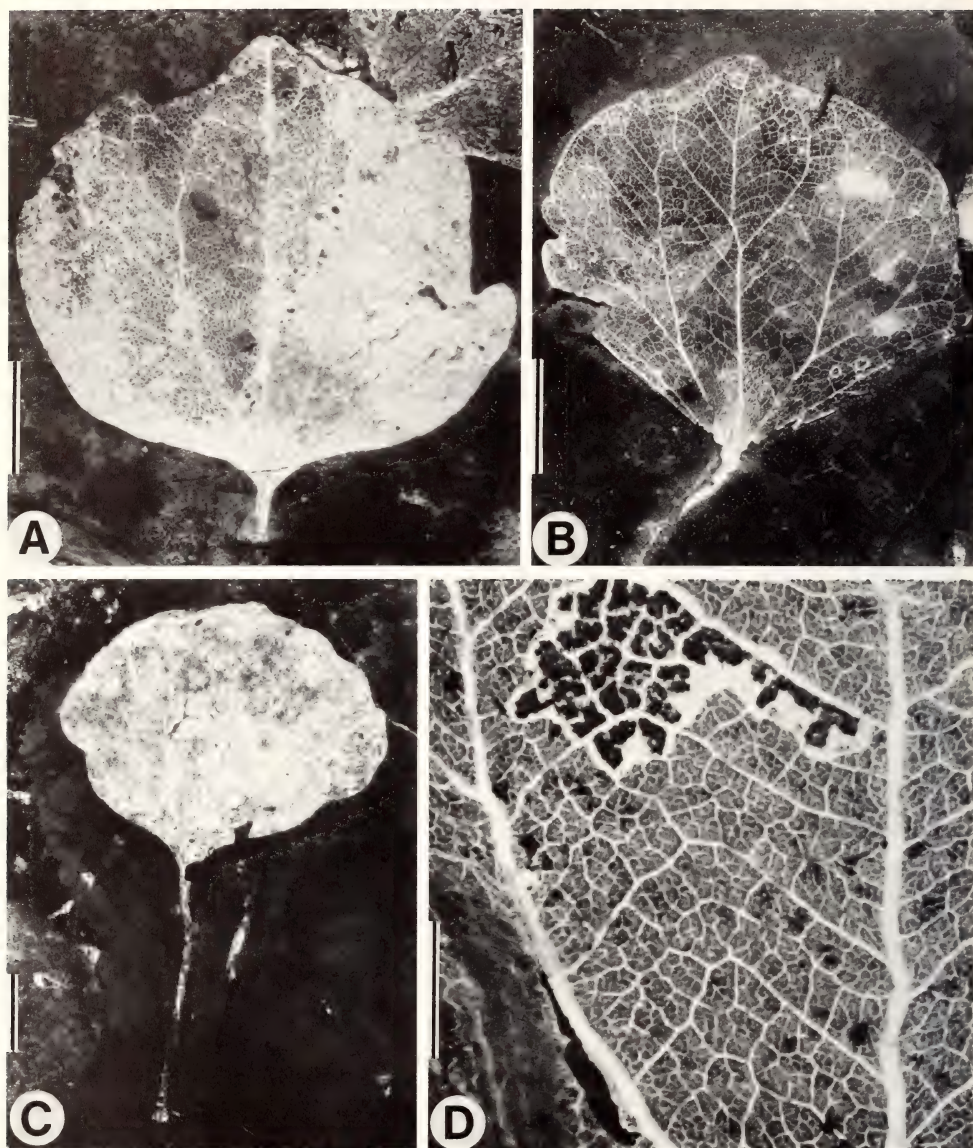
Fig. 9. Probable leaves of *Nordenskioldia borealis* Heer, "*Cocculus*" *flabella* (Newberry) Wolfe (Trochodendraceae). **A,** Leaf with actinodromous major venation and irregular marginal crenations, PP34201, ×1.5. **B,** Leaf showing major venation and predominantly entire margin, PP34204, ×1.5. **C,** Leaf showing long petiole, PP34205, ×1. **D,** Detail of intercostal venation in basal part of leaf, IU 7040, ×6. Scale bars: A–C, 1 cm; D, 3 mm.

been recovered from the Almont locality. Unequivocal infructescences and isolated fruits have not been recognized.

Type A leaves (fig. 11) are shallowly trilobed or deltoid with a lamina 6–15 cm long, 6.3–15.0 cm wide, and a length/width ratio of about 1.3 (fig. 11A–C). The leaf apex is acute, and the base obtuse to rounded. The petiole is up to 4.5 cm long with an expanded base. The leaf margin has regularly spaced distinctive sigmoidal teeth, typically with

→

Fig. 10. Fossil leaves and reproductive structures of *Nyssidium arcticum* (Heer) Iljinskaja (Cercidiphyllaceae). **A,** Leaf showing broad outline, actinodromous major venation and crenate margin, PP34209, ×1. **B,** Detail of counterpart of A showing fine venation and gland-tipped crenations, ×10. **C,** Leaf showing narrow outline, major venation, and
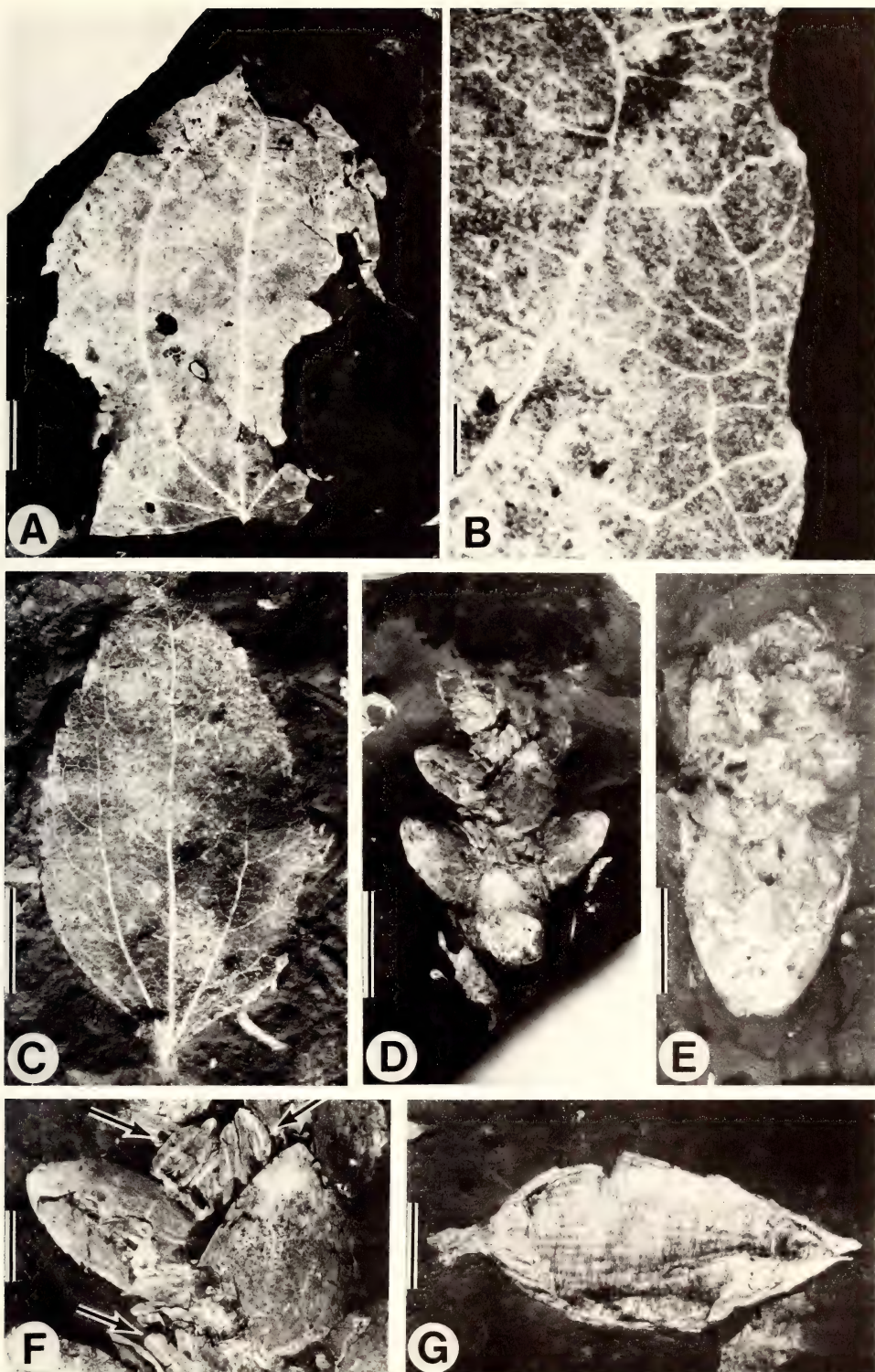
crenate margin, pp34321, ×1.5. **D,** Staminate inflorescence showing bracts and anthers, pp34423, ×1.5. **E,** Staminate inflorescence with overlapping bracts, pp34211, ×1.5. **F,** Detail of staminate inflorescence in D showing elongated anthers (arrows), ×3.3. **G,** Isolated follicle showing longitudinal striations and transverse fibers, pp34424, ×2.5. Scale bars: A, C–E, 1 cm; B, 1 mm; F, 3 mm; G, 5 mm.
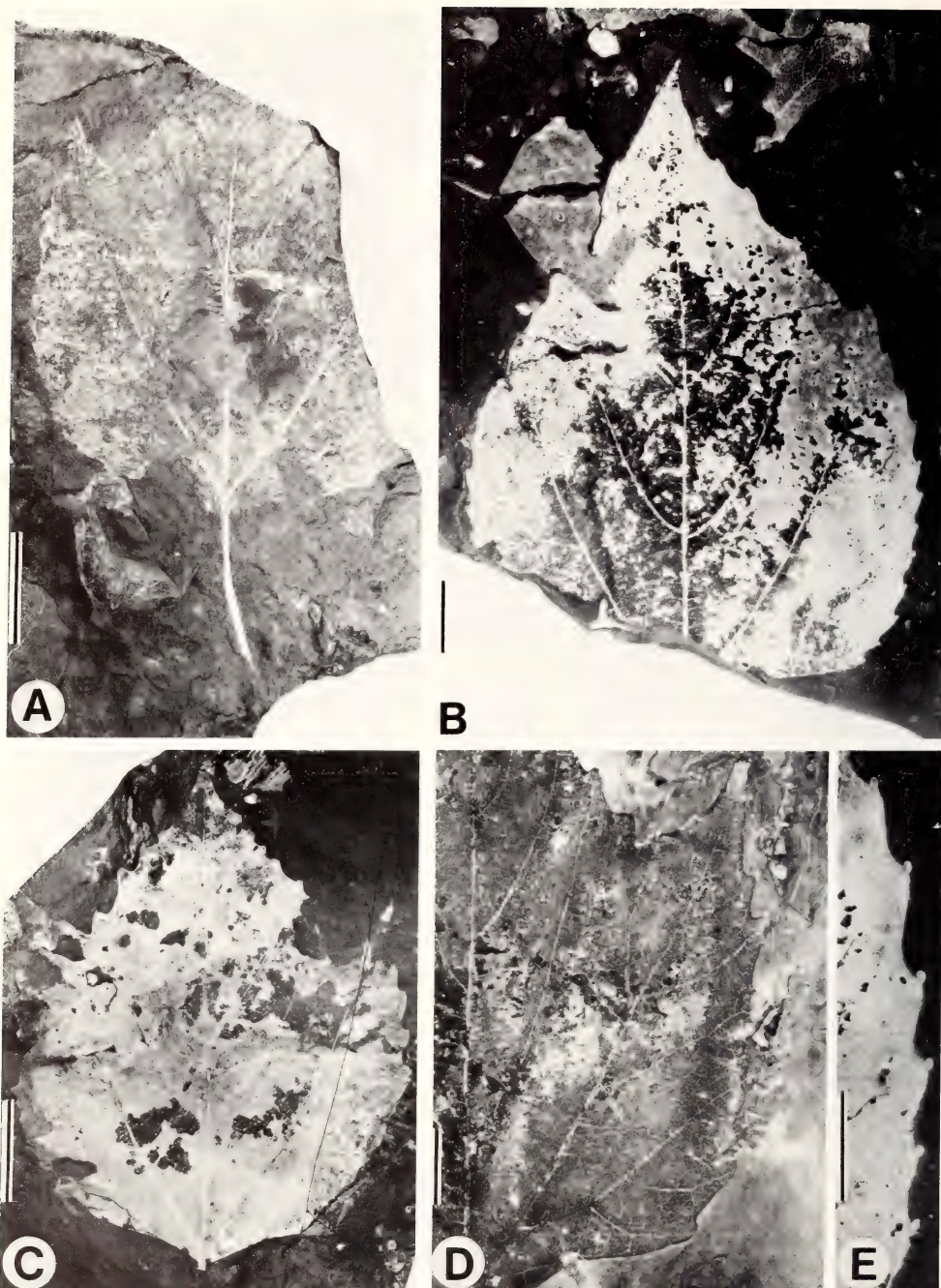
FIG. 11.   Fossil leaves of Platanaceae, cf. *Platanus*; type A. **A,** Leaf showing long petiole, trilobed lamina, three primary veins, and serrate margin, IU 5969, ×0.75. **B,** Leaf with very weakly developed lobes and prominent marginal teeth, PP34466, ×1. **C,** Leaf with trilobed lamina, actinodromous venation, lateral lobes, and prominent marginal teeth, PP34311, ×0.7. **D,** Portion of lamina showing divergence of secondary veins from the primary veins and orthogonal pattern of higher order venation, PP34310, ×1. **E,** Leaf margin from B showing prominent glandular teeth, ×3. Scale bars: A, C, 2 cm; B, D, 1 cm; E, 5 mm.
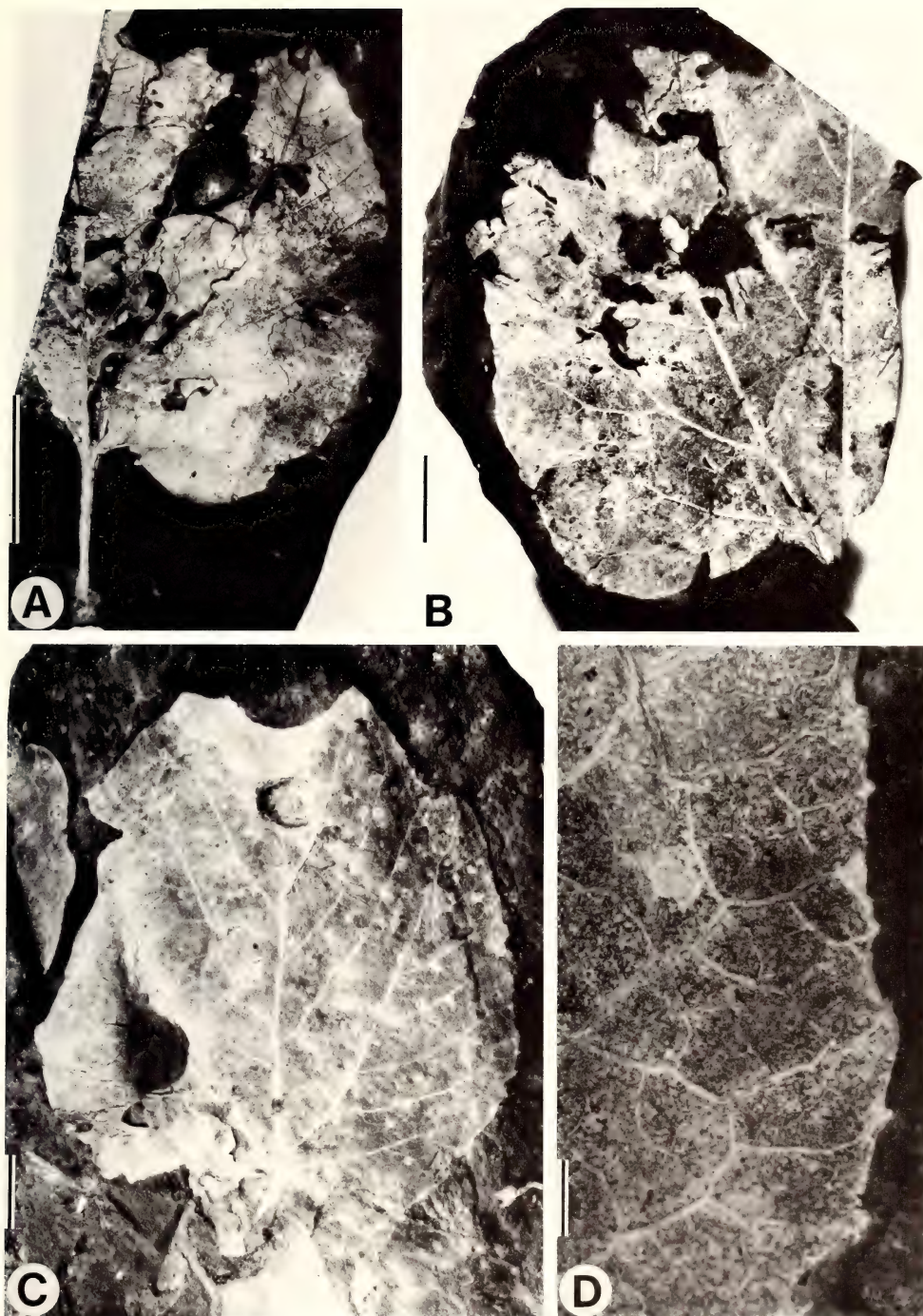
Fig. 12.   Fossil leaves of Platanaceae, cf. *Platanus*; type B. **A,** Leaf fragment showing cordate base, long petiole, and shallow marginal teeth, PP34470, × 0.5. **B,** Leaf fragment showing cordate base and details of venation, PP34488, ×0.6. **C,** Leaf showing weakly developed lobe and major venation; note unusual concave apex with fine teeth, PP34495, ×1. **D,** Detail of lateral margin from leaf in C showing higher order venation and glandular teeth, × 5. Scale bars: A, 4 cm; B, 2 cm; C, 1 cm; D, 2 mm.
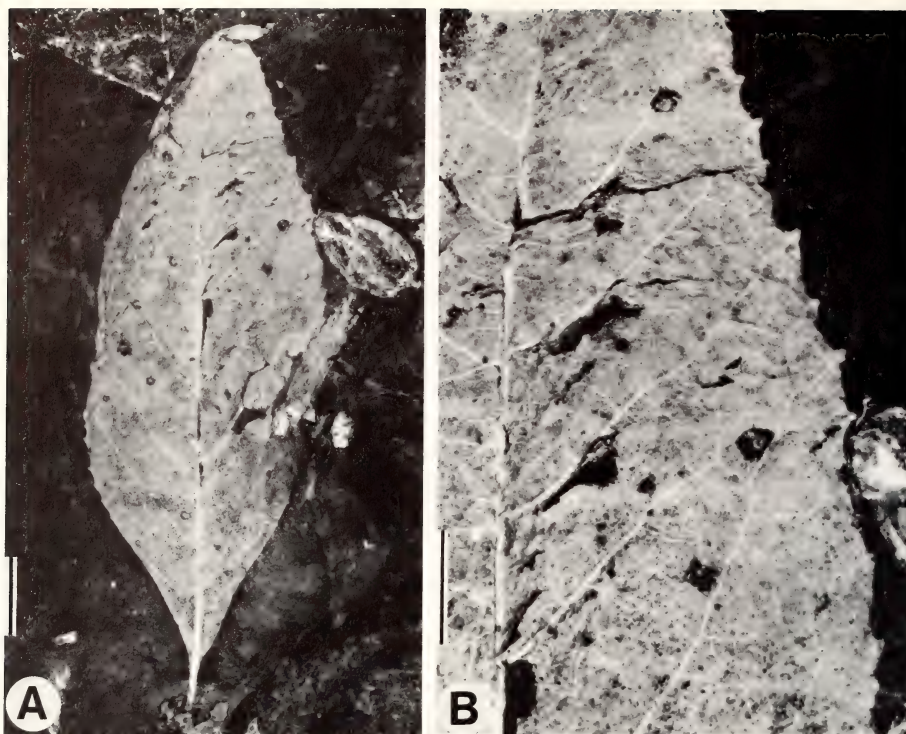
Fɪɢ. 13. Fossil leaves of Platanaceae, cf. *Platanus*; type C (*Dicotylophyllum flexuosa* (Newberry) Wolfe). **A,** Simple leaf, pp34486, ×1. **B,** Detail of intercostal and marginal venation from A; cf. Figure 12D, ×3. Scale bars: A, 1 cm; B, 5 mm.

a straight or concave adaxial margin and an acuminate abaxial margin (fig. 11A,B). Tooth apices have a prominent glandular tip (fig. 11E). Venation is actinodromous with three well-developed primary veins that diverge at, or slightly above, the base of the lamina (fig. 11A,C). Primary veins extend to the apex of each lobe. In some specimens the two lateral primary veins are produced by two distinct, unequal dichotomies of the central primary, and in all specimens examined the angle of divergence between the central and lateral primary veins is 30–40°. Lateral primary veins give off strong abmedial secondary veins to the marginal teeth, and the lowermost secondary veins also give rise to strong abmedial tertiary veins (fig. 11D). These secondary and tertiary veins are craspedodromous and terminate in the teeth. The central primary vein gives off secondary veins, typically at angles of 20–40°, that run into the central lobe of the lamina. The lowermost of these secondaries are often almost as well developed as the lateral primaries. Intercostal tertiary veins are thin and opposite-alternate percurrent. They show a "stitched" appearance as their course is modified

by the influence of quaternary veins. Higher order venation is orthogonal.

Type B leaves (fig. 12) are shallowly trilobed with a lamina up to 15 cm long, 16.5 cm wide, and a length/width ratio of 0.9–1.6 (fig. 12A–C). The normal form of the leaf apex is unknown, but the leaf base is distinctly cordate (fig. 12A–C). The petiole is up to 4.4 cm long, and basally expanded. The leaf margin has weakly developed, rarely sigmoidal, glandular teeth (fig. 12A–D). Venation is actinodromous and similar to that in type A leaves but varies from craspedodromous apically to semicraspedodromous basally. Secondary veins, and tertiary veins that are derived admedially from the lowermost secondary, become less distinct toward the margin, often forming camptodromous loops and dividing into tertiary and higher order veins that supply the teeth (fig. 12D). Intercostal tertiary veins are thin and opposite-alternate percurrent. They show a "stitched" appearance as their course is modified by the influence of quaternary veins. Higher order venation is orthogonal.

Type C leaves (fig. 13A,B) are represented by a
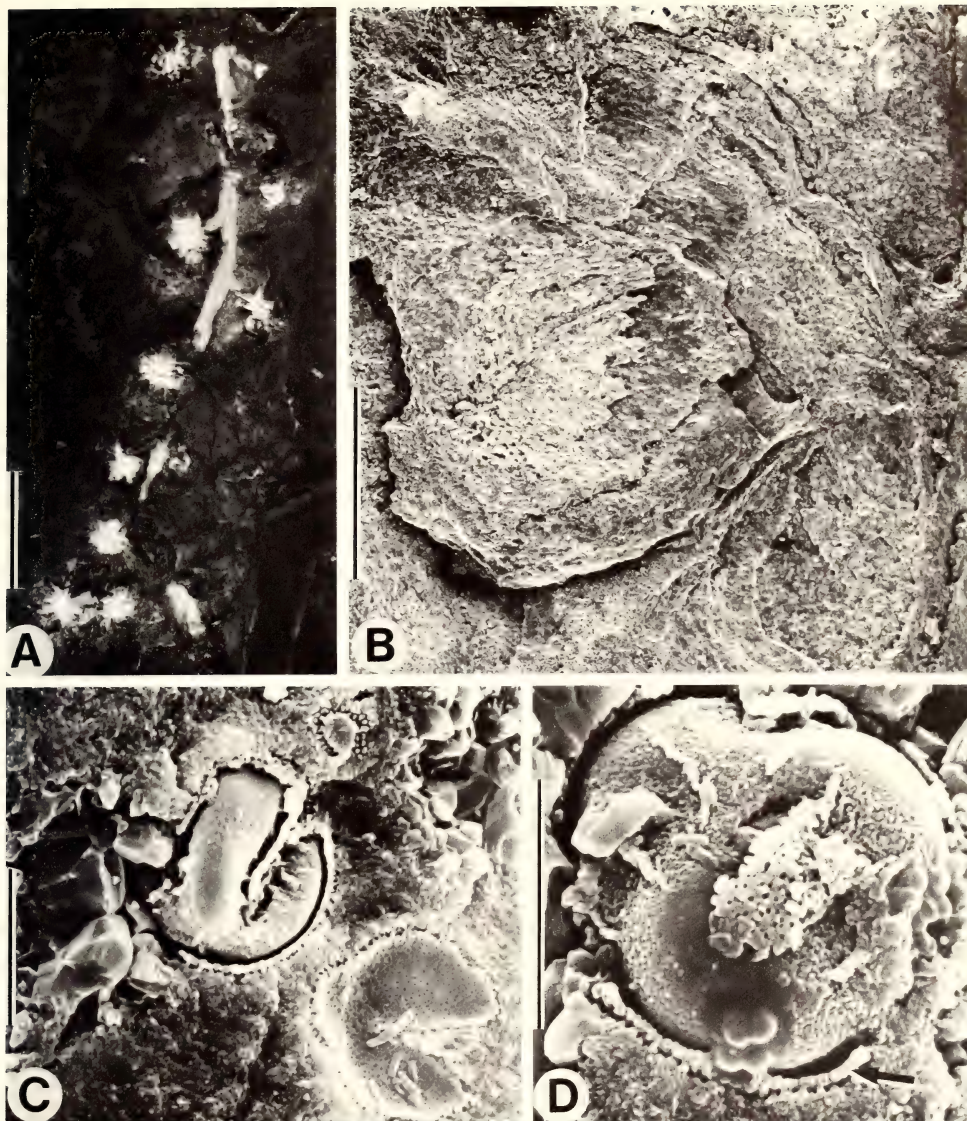
Fig. 14. Fossil staminate inflorescence of Platanaceae, cf. *Platanus*. **A,** Staminate inflorescence with lateral branches bearing clusters of flowers, PP34193, ×1.5. **B,** Scanning electron micrograph of cluster of flowers from the counterpart of inflorescence in A showing outline of a single flower, ×50. **C,** Scanning electron micrograph showing cast and molds of two pollen grains, ×2,000. **D,** Scanning electron micrograph showing detail of single pollen grain: note mold formed within the interstitium between the columellae (arrow), ×3,250. Scale bars: A, 1 cm; B, 0.5 mm; C, D, 10 μm.

single specimen from Almont. The lamina is narrowly elliptical, symmetrical, 8.5 cm long, 3.2 cm wide, with a length/width ratio of 2.8 (fig. 13A). The leaf apex is acuminate, and the base is cuneate, with a petiole at least 8 mm long. The leaf margin is finely and regularly serrate with small glandular teeth. Venation is pinnate with a straight midvein and 13 pairs of semicraspedodromous secondary veins. Secondaries undulate in course and branch near the margin with one branch entering a tooth

and the other curving distally to join a branch of the supra-adjacent secondary (fig. 13B). Tertiary veins arise at right angles to the secondaries, are opposite or alternate percurrent, and vary from straight and unwavering to "stitched" (zigzag). Quaternary and higher order venation forms a regular mesh of four- to five-sided areolae (fig. 13B). Areoles are small with few freely ending veinlets.

The staminate inflorescence consists of a central axis approximately 7.5 cm long bearing 10 clusters

of small flowers on short side branches of the inflorescence axis 1–2 mm long (fig. 14A). Floral structure is unknown but the manner in which the individual floral units may be differentiated with SEM (fig. 14B) suggests that the perianth was probably well developed. The flowers contain tricolpate pollen approximately 15 μm in equatorial diameter (fig. 14C,D). The nature of the exine surface is difficult to interpret because of the unusual preservation.

Platanus is the only extant genus in the Platanaceae and comprises approximately nine species in temperate to subtropical regions of North and Central America, southern Europe, and the Middle East. A single species, *Platanus kerrii* Gagnepain, occurs in tropical southeastern Asia. Although the fossil leaves and the staminate inflorescence from Almont show a general resemblance to those of extant Platanaceae, they show differences that caution against assignment to the extant genus.

Fossil leaves attributable to the Platanaceae are diverse and abundant in the fossil record from the mid-Cretaceous and throughout the Tertiary. Type A and B leaves fall within the broad concept of *Platanus raynoldsi* Newberry adopted by Brown (1962) and are also similar to certain specimens of *Ampelopsis acerifolia* (Newberry) Brown (Brown, 1962, pl. 31, figs. 2, 4, 6, pl. 51, fig. 9). They differ from *Platanus nobilis* Newberry in having fewer and less distinct lobes. They also differ from the foliage of two other Paleocene platanoids, *Platanites hebridicus* Forbes and "*Cissus*" *marginata* (Lesquereux) Brown (Crane et al., 1988; Crane, 1989), in having simple rather than pinnately compound leaves. Both type A and B leaves have outer primary veins with a much lower angle of divergence than is generally seen in extant *Platanus*, and in the living species the adult foliage typically has spinose teeth. Juvenile and developing leaves often have glandular teeth but the glands are usually lost early in development.

Type C leaves may be assigned to *Dicotylophyllum flexuosa* (Newberry) Wolfe and are widespread in the Paleocene of North America. They have been referred to many different extant genera, most recently *Quercus* (*Q. sullyi* Newberry; Brown, 1962) and *Meliosma* (*M. longifolia* (Heer) Hickey, 1977). The venation and glandular nature of the teeth differentiate the fossil from these modern genera, and suggest a relationship with *Platanus*. Although most extant species of *Platanus* have lobed leaves, the extant southeast Asian species *P.*

kerrii and the European Tertiary species *P. neptuni* (Kvaček, 1971) have simple elliptical laminae similar to those of *Dicotylophyllum flexuosa*. In addition, the thickness and course of the percurrent tertiary veins and nature of the intersecondary veins in type C leaves are both features shared with *Platanus kerri* and *Platanus neptuni*. Cuticular details would be useful in pursuing these comparisons further but have not been obtained so far from the Almont material.

Because only one specimen of a type C leaf is known from the Almont locality, it is possible that it was an aberrant form produced by the same species as the lobed foliage discussed above. The same kind of semicraspedodromy and marginal venation occurs in type B leaves. Seedling leaves of extant *Platanus* are often simple with pinnate veins. In addition, this situation occasionally occurs in more mature plants, for example, a specimen of extant *Platanus racemosa* Nutt. (US Herbarium sheet #1221000) shows an elliptical simple leaf borne on the same branch as more normal five-lobed forms, and we have observed the same feature in plants of several *Platanus* species grown under greenhouse conditions at Indiana University. At some localities in the Fort Union Formation *Dicotylophyllum flexuosa* is abundant and is often not associated with lobed forms. These occurrences suggest that simple leaves were the normal foliage in some extinct species and that forms existed in the Early Tertiary of North America similar to *Platanus neptuni* from the Tertiary of Europe. In North America *D. flexuosa* persists into the Early Eocene and is present in both members of the Golden Valley Formation (Hickey, 1977).

The fossil staminate inflorescence is unusual in bearing clusters of flowers on side branches of the inflorescence axis (fig. 14A). In extant *Platanus* the heads of staminate flowers are sessile on the main inflorescence axis. The pollen in the fossil flowers (15 μm equatorial diameter) is smaller than that in extant species of *Platanus* (16–27 μm), and the perianth is apparently better developed. The occurrence of small pollen and a well-developed perianth in other early Tertiary and Cretaceous Platanaceae (Crane et al., 1986; Manchester, 1986; Friis et al., 1988) is suggestive of insect pollination.

In addition to the staminate inflorescence, a single probable platanoid androecium (IU 7064) comparable to *Macginistemon* (an adhering group of five platanaceous stamens; Manchester, 1986) has also been identified from the Almont locality.
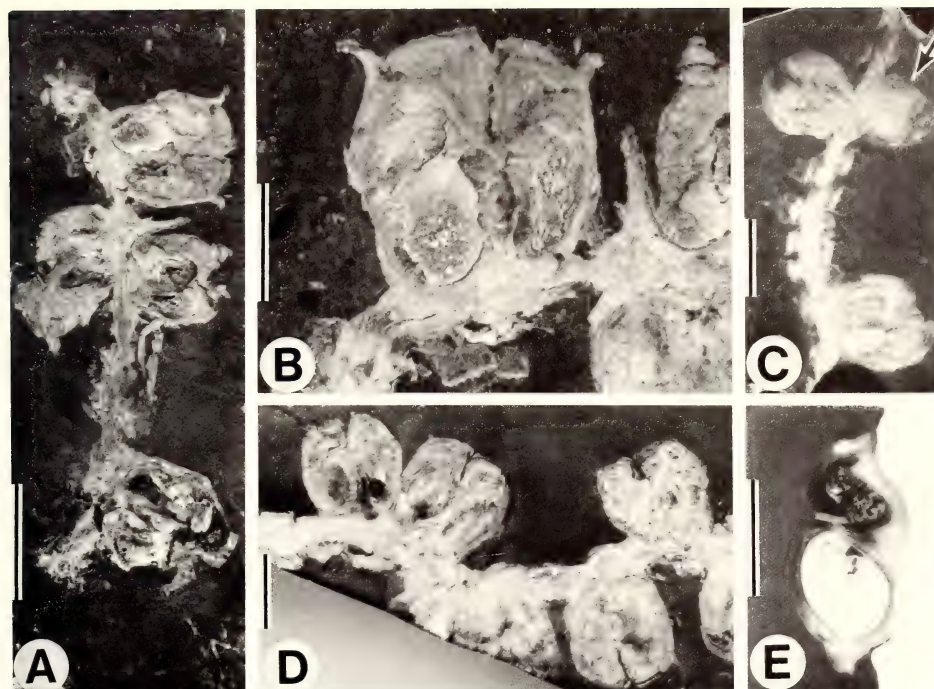
FIG. 15. Fossil infructescences and fruits of Hamamelidaceae. **A,** Portion of infructescence with four attached fruits, ɪu 5977, ×1.5. **B,** Single fruit from the infructescence in A showing bilocular fruit, suture between the carpels, and two diverging styles, ×3. **C,** Portion of infructescence showing three attached fruits; note separate flanges, possibly representing aborted gynoecia, along the infructescence axis: arrow indicates fruit sectioned and illustrated in E, ɪu 5978, ×1. **D,** Portion of infructescence showing seven attached fruits, pp34417, ×1. **E,** Transverse section through fruit in C showing two locules separated by a transverse septum, ×3. Scale bars: A, C, D, 1 cm; B, E, 5 mm.

Hamamelidaceae. Figure 15.

Infructescences consist of at least 10 robust fruits that are sessile along a stout axis up to 7 cm long (fig. 15A,D). The infructescence axis occasionally shows distinct lateral flanges (fig. 7C) possibly representing aborted gynoecia. In longitudinal fractures (fig. 7B) the fruits are roughly square, 10–12 mm long, 10–12 mm wide, with convex sides. The distal face is convex with a protruding, recurved, persistent style at either end. Fruits are elliptical in transverse section (fig. 7E), about 5 mm thick, and show two more or less circular locules. Dehiscence was apical by a split bisecting each of the locules, dividing each of the persistent styles into two halves. The locules are ovoid, 5–6 mm long, and 3.0–3.5 mm in diameter, and oriented parallel to the central fruit axis, but more or less confined to the lower half of the fruit. All of the specimens that we examined appear to have dehisced and shed the seeds prior to deposition.

These fruits are similar to those of extant Hama-

melidaceae in the bilocular construction and the manner in which the plane of dehiscence bisects each of the persistent styles. It is possible that the fruits ejected the seeds explosively as in the subfamily Hamamelidoideae (Endress, 1987). Although none of the fruits show seeds *in situ,* isolated asymmetric ellipsoidal seeds, morphologically similar to those of extant Hamamelidoideae, occur as very rare elements in the Almont collections (p. 42, fig. 27E-G). These seeds have dimensions similar to those of the fruit locules and may have been produced by the same species.

The extant family Hamamelidaceae includes approximately 30 genera. Probable hamamelidaceous flowers are known from the Upper Santonian or Lower Campanian of southern Sweden (Friis, 1985), and hamamelidaceous seeds have been described from the Maastrichtian (Knobloch & Mai, 1984, 1986). Seeds of the Hamamelidoideae are widespread from the Eocene onwards (Takhtajan, 1974; Collinson, 1982, 1983, 1984; Gregor, 1982; Mai & Walther, 1985).

Betulaceae

Palaeocarpinus sp. Figures 16–18A,B.

Infructescences are up to 11 cm long and consist of about 30 fruits evenly distributed along the infructescence axis (fig. 16A). Fruits consist of a small, broadly ovate nutlet 3–5 mm long, 3–4 mm broad, borne between two deeply divided spinose involucral bracts (fig. 16B). Involucral bracts vary in size along the infructescence axis, the largest involucres being in the center with smaller involucres at either end (fig. 16A).

Associated leaves are simple, with a broadly elliptical to broadly ovate lamina 5–13 (typically 7) cm long, and 4–10 (typically 5) cm wide, and a length/width ratio of about 1.5 (fig. 18A). The leaf apex is obtuse, the base cordate or rounded, and the margin serrate. The petiole is 2–5 cm long and slightly expanded proximally. Venation is pinnate, typically with about eight craspedodromous secondary veins arising from the midrib at angles of about 40°. The lowermost secondaries arise at the extreme base of the lamina at a broader angle than the more apical secondary veins. A pair of veins of intermediate secondary–tertiary order also diverge from this point at a high angle to the midvein. Secondary veins curve upwards as they enter the teeth producing abmedial tertiary veins close to the margin that supply the subsidiary teeth (fig. 18B). Intercostal tertiary veins are percurrent between the secondaries and arise at approximately 90° (fig. 18A). Quaternary and higher order venation delimits small polygonal areolae with freely ending veinlets.

Associated staminate inflorescences are clustered in groups of three at the apex of vegetative axes (fig. 17A). Inflorescences are typically 3–5 mm wide, but vary considerably in length and may be up to 13 cm long (fig. 17A–C). Each catkin consists of overlapping, helically arranged, ovate primary bracts, typically 2 mm long and 1.5 mm broad (fig. 17A). Each primary bract subtends a cluster of stamens, with anthers containing abundant triporate pollen (fig. 17D–F). Pollen grains are approximately 25 μm in equatorial diameter with aspidote apertures and finely rugulate ornamentation (fig. 17E). Similar pollen is abundant as dispersed grains in palynological preparations from the Almont matrix. They are readily separated from dispersed triporate grains of Juglandaceae (also present at the Almont locality) by their larger size and fine rugulate ornamentation

that contrasts with the distinct, evenly distributed coni of juglandaceous pollen.

Palaeocarpinus infructescences and fruits are among the most abundant components of the Almont flora. *Palaeocarpinus* was originally described based on isolated fruits (*P. laciniata* Crane) from the Paleocene Woolwich and Reading Formation of southern England (Crane, 1981a,b). The Almont material provides well-preserved complete infructescences and substantially adds to our understanding of this extinct betulaceous plant. The discovery of *Palaeocarpinus* at Almont has also led to its recognition in other Paleogene localities in North America. These include five localities in the Fort Union Formation of Wyoming and Montana (see Brown, 1962, pl. 67, figs. 39–42, 47), a locality in the Middle Eocene of British Columbia, and another in the Middle Eocene of Washington (Crane, unpubl.). There is also a probable further record of *Palaeocarpinus* (*Atriplex borealis* Laurent, 1912) in the Paleocene of Menat, France. The shape and size of *Palaeocarpinus* bracts at these different localities varies considerably. The material previously described by Brown (1962) has deeply divided involucres resembling those of the Almont material.

Betulaceous leaves and staminate inflorescences are common at Almont and were probably produced by the *Palaeocarpinus* plant. The same association of infructescences, leaves, and staminate inflorescences is also known to occur at two localities in the Fort Union Formation of Wyoming (USGS localities 9109, 9438; Brown, 1962). The leaves are similar to those described by Brown (1962) as *Betula stevensoni* Lesquereux and *Corylus insignis* Heer.

The extant Betulaceae comprises six genera distributed between two tribes, the Betuleae, including *Alnus* and *Betula,* and the Coryleae, including *Carpinus, Corylus, Ostrya,* and *Ostryopsis. Palaeocarpinus* displays an unusual combination of the characters of several betulaceous genera. The nutlets are similar in size and anatomical details to those of *Carpinus, Ostrya,* and *Ostryopsis,* and the elongated infructescences are similar to those of *Carpinus* and *Ostrya* (Crane, 1981b). However, the arrangement and form of the bracts subtending each nutlet is unlike the involucre of these three genera and much more similar to the bracts of some extant species of *Corylus,* for example, *C. ferox* Wall. (fig. 16C) and *C. heterophylla* Fisch. Interpreted phylogenetically *Palaeocarpinus* exhibits both the primitive nutlet and bract condi-
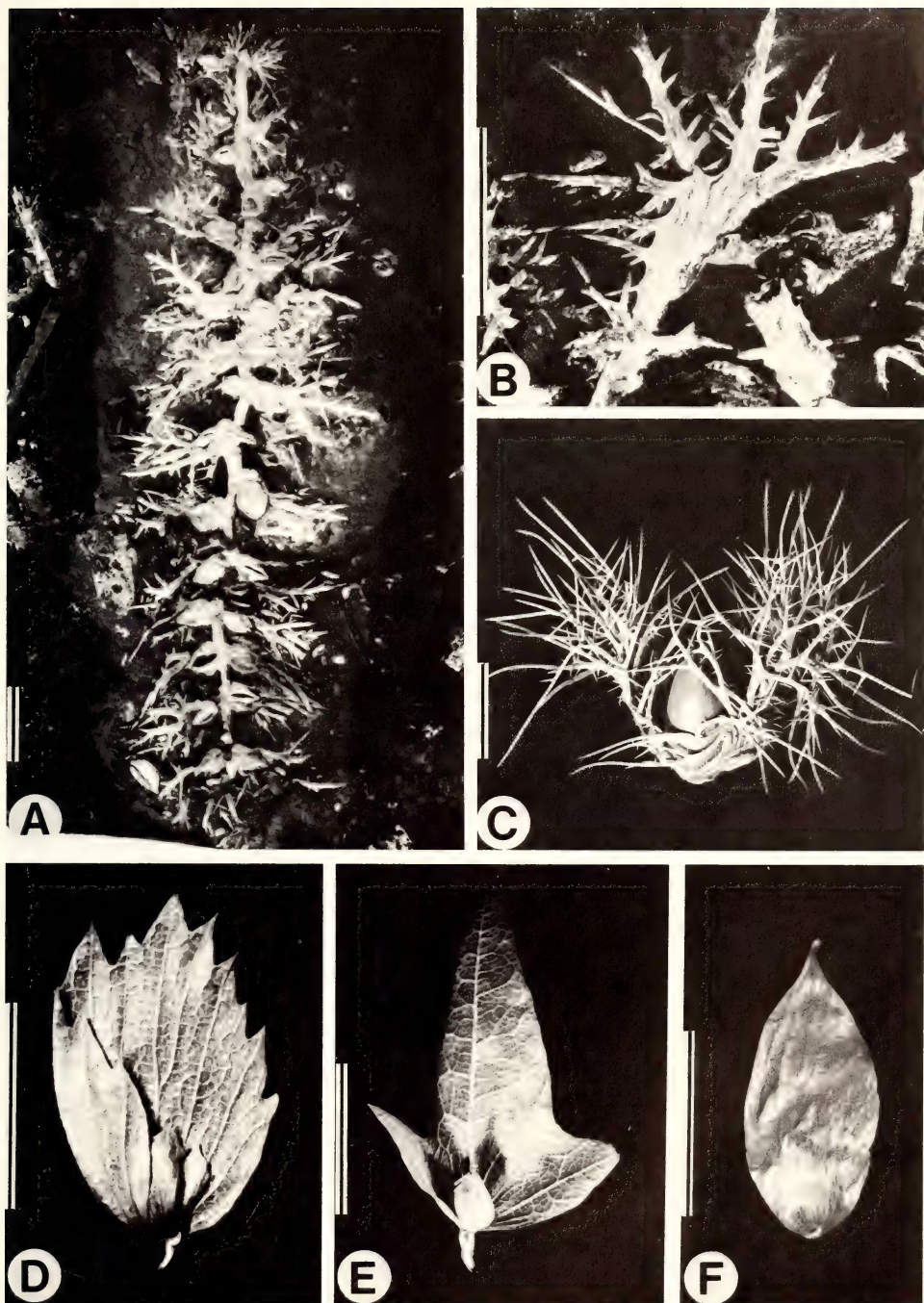
Fig. 16. Fruits of *Palaeocarpinus* and extant Coryleae (Betulaceae). **A,** Fossil *Palaeocarpinus* infructescence with numerous nutlets and associated pairs of spinose bracts, PP34079, ×1. **B,** Fossil *Palaeocarpinus*, detail of a spinose bract, PP34080, ×2. **C,** Fruits of extant *Corylus ferox* Wall. showing nut surrounded by an involucre of two spinose bracts, ×1.25. **D,** Fruit of extant *Carpinus japonica* Bl. showing arrangement of large and small bract, ×2.75. **E,** Fruit of extant *Carpinus caroliniana* Walt., ×2. **F,** Fruit of extant *Ostrya carpinifolia* Scop., ×2.5. Scale bars: A, C–F, 1 cm; B, 1.25 cm.
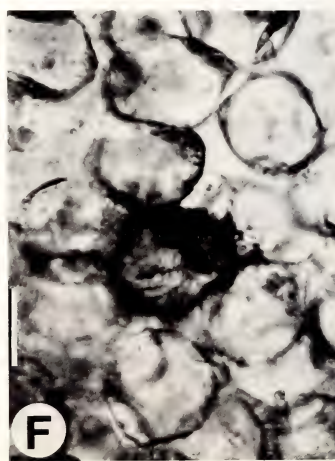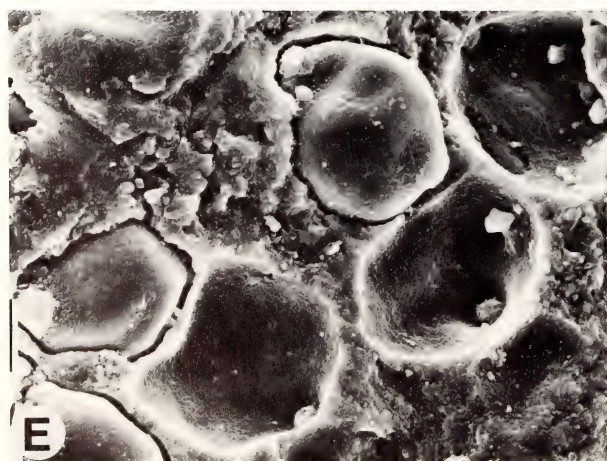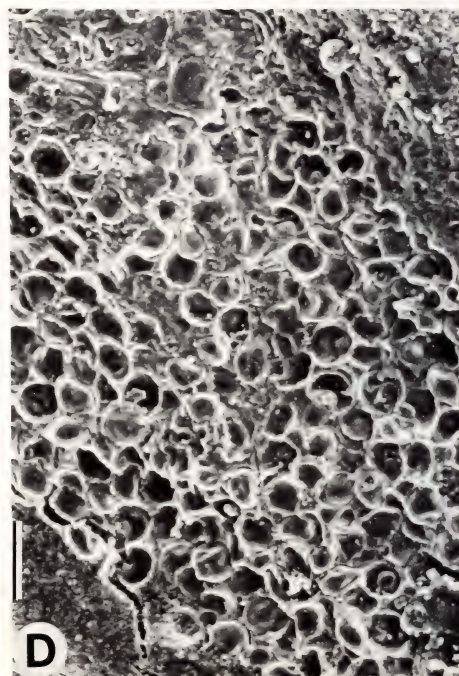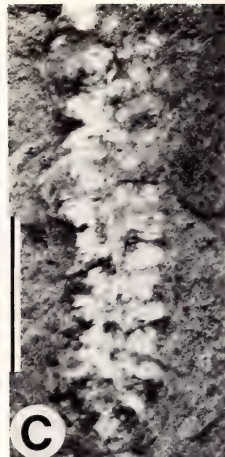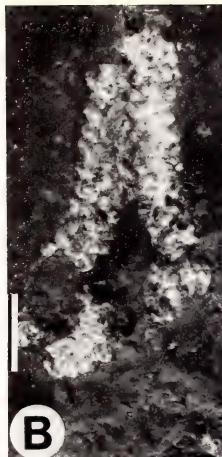
tion in the Coryleae. *Corylus* is more specialized in its large, animal-dispersed nuts and the loss of an elongated infructescence (the infructescence is also reduced in *Ostryopsis*). Conversely, *Carpinus* and *Ostrya* have retained the primitive nutlet condition and elongated infructescence, but are more specialized than primitive species of *Corylus* in the morphology of their involucre. *Palaeocarpinus* is a generalized member of the Coryleae and is similar to what might be predicted as a hypothetical common ancestor for the tribe.

The Betulaceae has a fossil record that extends from the Upper Cretaceous through the Tertiary. Dispersed pollen with characters diagnostic of extant *Alnus* is recorded from the Santonian and Campanian of Japan (Takahashi, 1974; Miki, 1977). Pollen of *Betula* is reported from the Senonian (Jarzen & Norris, 1975; Miki, 1977) and the genus is clearly recognizable on the basis of associated leaves, infructescences, fruits, inflorescences, and pollen in the Middle Eocene (Crane & Stockey, 1987). The paleobotanical evidence strongly suggests that the Betuleae are the more ancient of the two extant tribes in the family. Unequivocal remains of Coryleae do not appear until the Paleocene when both *Corylus* nuts (Seward & Holltum, 1924; Brown, 1962; Koch, 1978) and *Palaeocarpinus* are first recorded. The distinctive involucres of extant *Carpinus* (fig. 16D,E) and *Ostrya* (fig. 16F) are not recorded until the Eocene (Szaferowa, 1958; Tanai, 1972; Mai, 1981) and Oligocene (Chaney, 1927; Manchester & Crane, 1987), respectively. Fruits and associated leaves of *Asterocarpinus,* an extinct member of the Coryleae, are also known from the Oligocene (Manchester & Crane, 1987). *Palaeocarpinus* therefore occupies a key position in the evolution of the Betulaceae as one of the earliest representatives of the tribe Coryleae.

Juglandaceae

Cyclocarya brownii Manchester & Dilcher.
Figures 18C,D,F,G, 19.

Fruits borne on slender pedicels, 2–3 cm long (fig. 18C). Each fruit consists of a nutlet surround-ed by a disk-like wing 2.0–3.5 cm in diameter with radiating dichotomous, occasionally reticulate, venation (fig. 18C,D). The nutlet is more or less square in plan view, 4.5–6.0 mm in diameter, with two prominent external ridges that divide the surface into four more or less equal parts (fig. 18C). Nutlets taper apically into a stout bifurcate style (fig. 18F; Manchester & Dilcher, 1982). Internally a primary and secondary septum divides the locule into four basal lobes (fig. 18D).

Associated leaves are compound. Leaflets are symmetrical to asymmetrical, rarely obovate, typically broadly elliptical (fig. 19A) to broadly ovate and often more or less parallel sided (fig. 19C). Lamina 8–14 cm long, 3–7 cm wide, length/width ratio 1.5–2.5. The apex is acute to acuminate and the base obtuse to rounded. The margin is regularly serrate with numerous closely spaced fine teeth (fig. 19B), the tooth apices typically forming angles of about 90°. Venation of terminal and lateral leaflets is pinnate and semicraspedodromous, typically with about 18 secondary veins arising from the midrib at angles of 50–60°. Secondary veins typically turn upward just before the teeth to form weakly differentiated marginal loops. Teeth are supplied by abmedial tertiary veins that arise from the secondaries and enter the teeth submedially. Tertiary veins are percurrent between the secondaries arising at approximately 90°. Quaternary and higher order veins delimit small orthogonal areolae with branched, freely ending veinlets.

Cyclocarya (Juglandaceae) is an extant genus with a single living species *C. paliurus* (Batalin) Iljinskaja in the mixed mesophytic forest of eastern Asia. The genus is known from various occurrences in the Oligocene and Pliocene of Europe and Asia, as well as the Paleocene of Montana, North Dakota, and Wyoming (Manchester & Dilcher, 1982; Manchester, 1987).

Cyclocarya brownii fruits are very abundant in the Almont flora. They were first described from other localities in the Fort Union Formation by Brown (1962), who assigned both the fruits and associated leaves to *Pterocarya* (*sensu lato*). Noting the recognition of extant *Cyclocarya* as a genus distinct from *Pterocarya* (Iljinskaja, 1953), Manchester and Dilcher (1982) assigned the fossil fruits

---

←

Fɪɢ. 17. Fossil staminate inflorescences of Betulaceae, cf. *Palaeocarpinus.* **A,** Twig with three attached inflorescences, ᴜɴᴅ 13057, ×1. **B,** Pair of staminate inflorescences, ᴘᴘ34191, ×1. **C,** Staminate inflorescence showing clusters of exposed anthers, ᴘᴘ34194, ×4. **D,** Scanning electron micrograph of fractured anthers from C showing casts and molds of numerous pollen grains, ×200. **E,** Scanning electron micrograph showing detail of casts and molds of pollen grains from C; note mold of pollen surface sculpture, ×1,000. **F,** Light micrograph of thin section of staminate catkin showing pollen grains, ᴘᴘ 34602, ×500. Scale bars: A, B, 1 cm; C, 5 mm; D, 50 µm; E, 10 µm; F, 20 µm.
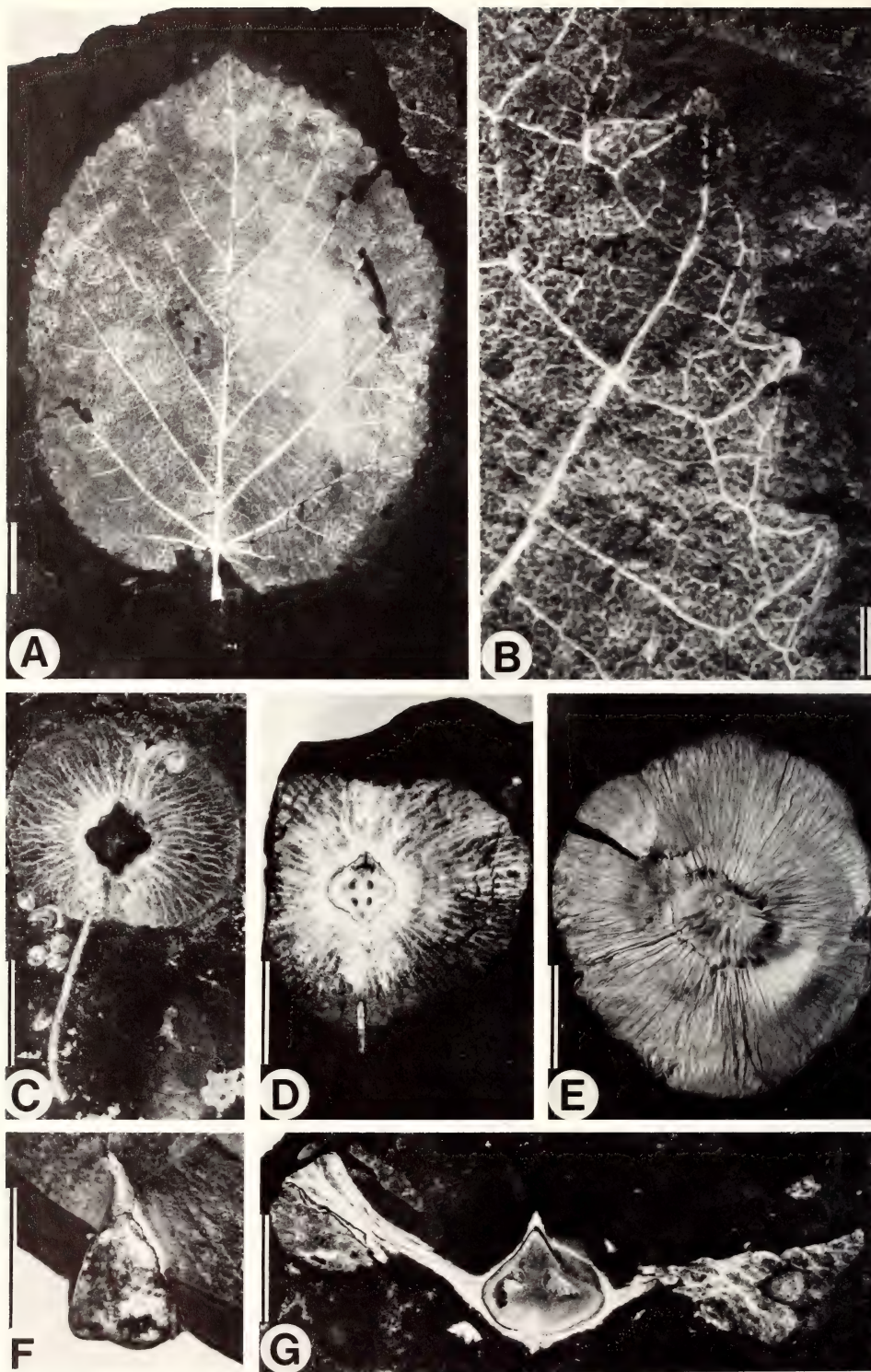
FIG. 18.   Fossil leaves of Betulaceae, cf. *Palaeocarpinus,* and fruits of extant and fossil *Cyclocarya* (Juglandaceae). **A,** Betulaceous leaf showing outline and major venation, PP34212, ×1. **B,** Detail of betulaceous leaf margin showing primary and subsidiary teeth and marginal venation, PP34565, ×10. **C,** Fruit of *Cyclocarya brownii* Manchester & Dilcher showing pedicel, and central nut surrounded by a circular wing, PP34117, ×1.5. **D,** Fruit of *Cyclocarya brownii*
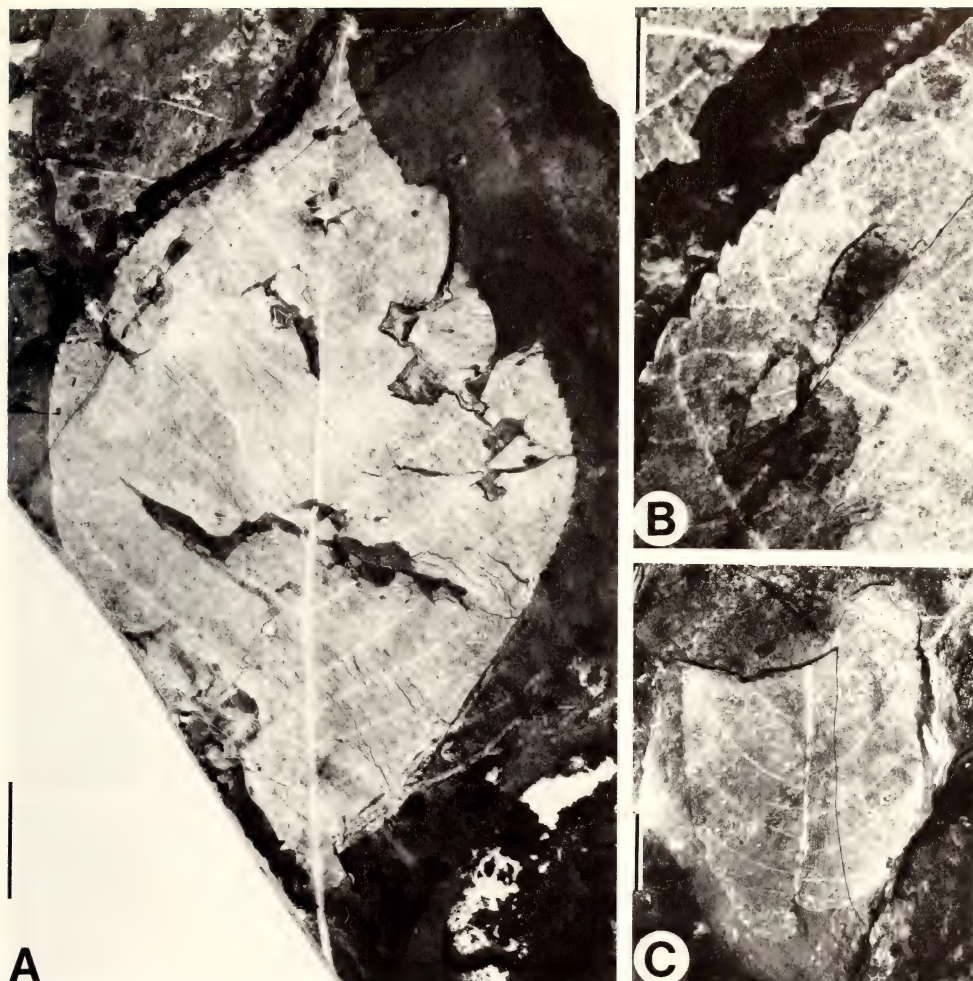
FIG. 19. Fossil leaflets of Juglandaceae, cf. *Cyclocarya*. **A,** Large terminal leaflet, PP34313, ×0.75. **B,** Detail of marginal venation from A; note camptodromous secondary veins, ×2.5. **C,** Small lateral leaflet with asymmetric base, PP34463, ×1. Scale bars: A, 2 cm; B, 5 mm; C, 1 cm.

to *Cyclocarya brownii*. Since the original description of fruits from Almont (Manchester & Dilcher, 1982), at least 200 additional specimens have been collected. These confirm the previous description but also provide new information on the pedicel (Manchester, 1987). The pedicel varies from 2 to 3 cm in length in *C. brownii* (fig. 18C), whereas in extant *C. paliurus* the pedicel is only 1–3 mm long and the fruits are subsessile on the infructescence axis. The basic organization of the fossil fruits from Almont is identical to that in extant *Cyclocarya*

paliurus (fig. 18E) and the only specific differences that have been noted are that the fossil has pyramidal rather than lensoidal nutlets, a basal rather than equatorial wing attachment (fig. 18G), consistently four-lobed rather than two- or four-lobed seeds, and longer pedicels.

In view of the abundance of *Cyclocarya* fruits at Almont it is interesting that juglandaceous leaflets are not common in the flora (Table 1). This presumably reflects differential transport of the winged *Cyclocarya* fruits prior to deposition. The

←
with nutlet sectioned to show the four basal lobes of the locule cavity, PP34212, ×1.5. **E,** Fruit of extant *Cyclocarya paliurus* (Batalin) Iljinskaja, ×1.5. **F,** Longitudinal view of *Cyclocarya brownii* nutlet showing triangular profile and stout persistent style, PP34468, ×4. **G,** Fruit of *Cyclocarya brownii* fractured obliquely and longitudinally showing submedial attachment of wing to nutlet, PP34144, ×3. Scale bars: A, C–E, 1 cm; B, 1 mm; F–G, 5 mm.

juglandaceous leaflets in the flora are similar in their venation and organization to those of extant *Pterocarya* and *Cyclocarya,* although they lack the apiculate teeth seen in many specimens of extant *C. paliurus.* Brown (1962) attributed similar leaves from other localities in the North American Paleocene to *Pterocarya hispida* Brown. *Pterocarya (sensu stricto)* (excluding *Cyclocarya*) is unknown on the basis of fruits in the Paleocene, and the occurrence of a single kind of juglandaceous fruit and leaflet at Almont adds to the evidence that at least some of the "*Pterocarya*" *hispida* leaflets were produced by the *Cyclocarya brownii* plant.

Juglandaceous staminate inflorescences have not so far been recovered from the Almont locality. Small triporate juglandaceous pollen is, however, abundant in the dispersed palynoflora (Manchester, 1987, fig. 37H,I). If this pollen was produced by the *C. brownii* plant, and there is no evidence of other juglandaceous species in the flora, then it differs from the larger, predominantly tetraporate (rarely triporate) grains of extant *Cyclocarya.* Small triporate pollen is widely regarded as primitive in the Juglandaceae, and the apparent discrepancy is probably explained by mosaic evolution involving the retention of a primitive pollen feature in the *Cyclocarya brownii* plant.

The extant Juglandaceae includes eight modern genera, and has an excellent fossil record in the Early Tertiary of the Northern Hemisphere (Crepet et al., 1975; Dilcher et al., 1976; Dilcher & Manchester, 1986; Manchester, 1987). The occurrence of *Cyclocarya* in the Paleocene is significant as the earliest record of an extant genus of the family. All other juglandaceous fruits from the Paleocene, including *Casholdia* (Crane & Manchester, 1982), *Juglandicarya* (Brown, 1962; Manchester, 1987), and *Polyptera* (Manchester & Dilcher, 1982), are significantly different from those of living representatives. Other extant genera of Juglandaceae do not appear in the fossil record until the Eocene (Manchester, 1987).

Myrtaceae

?*Psidium* sp. Figure 20A–E.

Fruits consist of a compressed globular parenchymatous mass 1–2 cm in diameter filled with numerous small seeds (fig. 20A,B). A very thin poorly preserved fruit wall, about 90 μm thick, surrounds the seed-bearing tissue (fig. 20B). The seeds are broadly reniform and somewhat flattened laterally. They are 1.5–2.0 mm long, 1.3–1.6 mm wide, and 0.8–1.2 mm thick, and contain a curved C-shaped embryo (fig. 20C). The dorsal side of the seed has a layer of columnar cells 90–125 μm thick. The ventral side is made up of isodiametric cells 10–12 μm in diameter traversed by a raphe bundle about 75 μm in diameter (fig. 20D,E). The distinctive seeds are commonly found dispersed within the sediment (fig. 20C).

The fruit and seeds of this species closely resemble those of extant *Psidium guineense* Sw (fig. 20F). However, the extant species has a thicker fruit wall and does not possess the dorsal layer of columnar cells seen in the fossil seeds. *Psidium* has about 140 extant species distributed in tropical America and the West Indies (Willis, 1973) and is known for its edible fruits such as the guava (*P. guajava* L.). Although securely placed in the Myrtaceae, subfamily Myrtoideae, determination of the precise systematic position of this fruit will require detailed anatomical comparison with a larger sample of extant species in *Psidium* and related genera. We have not observed this fruit type in other Paleocene floras and as far as we are aware it has not previously been recorded.

Cornaceae

Cornus sp. Figure 20G–I.

Endocarps ovoid, 7–9 mm long and 5.5–7.0 mm wide, with a slight apical (stylar) depression. Endocarp wall 0.3 mm thick composed of cells with strongly sinuous walls giving a finely rugulate appearance in longitudinal fractures (fig. 20G). Endocarp wall containing numerous irregularly ovoid cavities approximately 0.4 mm long and 0.2 mm wide. A specimen sectioned transversely (fig. 26I) shows three locules delimited by radial septa. Each locule contains a single seed.

These endocarps correspond closely in morphology to "stones" of the extant genus *Cornus,* and the numerous cavities in the endocarp and the apical depression are diagnostic of the "cornelian cherry" subgroup (Eyde, 1988). Among fossil fruits the Almont specimens are closely similar to those of *Cornus ettingshausenii* (J. S. Gardner) Eyde from the lower Eocene London Clay flora of southern England (illustrated as *Dunstania* by Reid & Chandler, 1933, p. 459, pl. 25, figs. 41–47). In diagnosing the genus *Dunstania,* Reid and Chandler
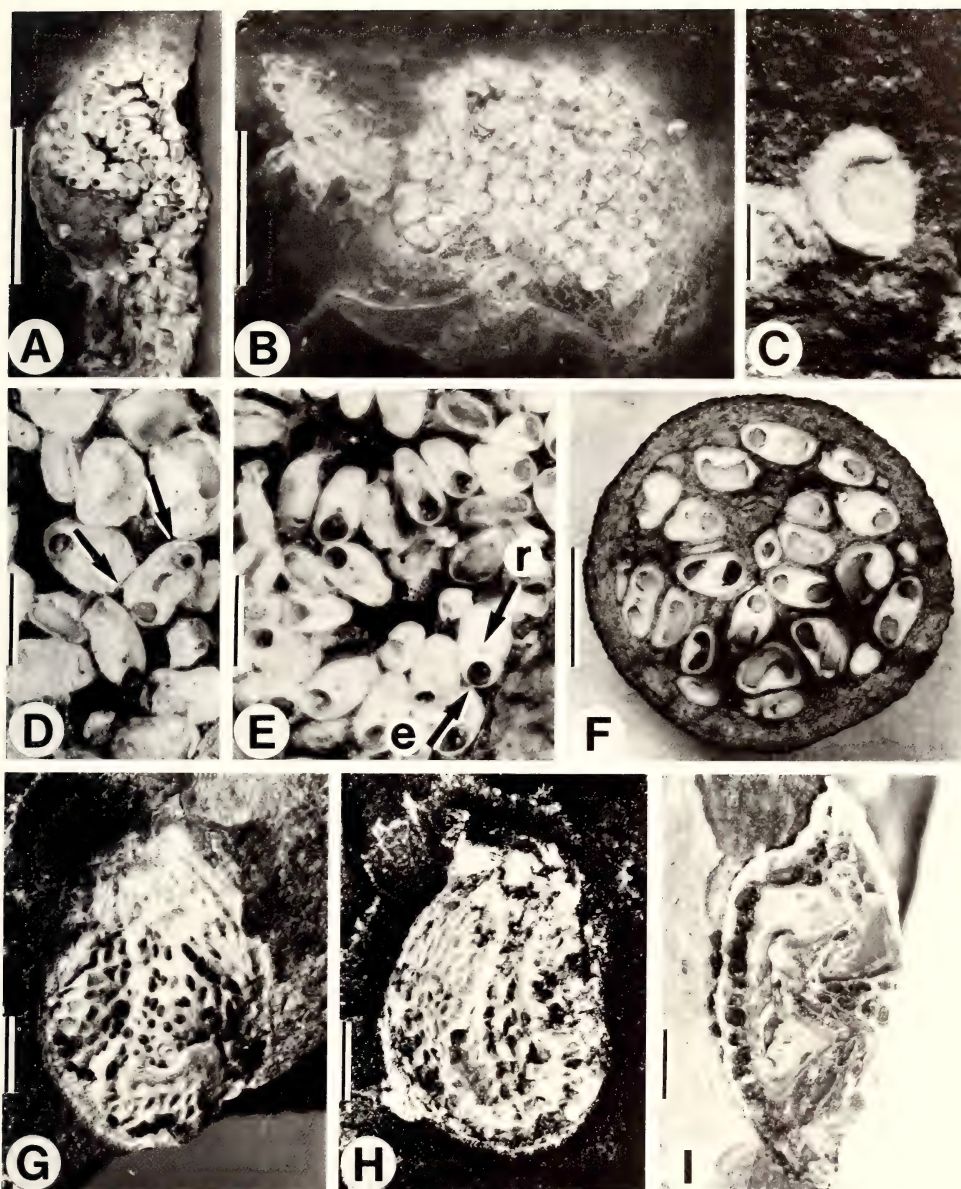
Fig. 20. Fruits of fossil and extant *Psidium* (Myrtaceae) and fossil *Cornus* (Cornaceae). **A,** Incomplete fossil fruit of *Psidium* showing flask-shaped mass of small seeds, IU 6177, ×2. **B,** Fossil fruit of *Psidium* showing small seeds partially enclosed by a membranous covering, PP34465, ×2. **C,** Lateral view of isolated fossil seed of *Psidium* showing the curved C-shaped embryo, UND 13058, ×10. **D,** Section through several fossil seeds of *Psidium*: note seed in which both ends of the curved embryo are visible (arrows), PP34560, ×6. **E,** Section through fossil seeds in A showing asymmetrically positioned embryo (E) and position of the raphe (R), ×6. **F,** Section through a fruit of extant *Psidium guineense* Sw (Arnold Herbarium, *Williams & Molina 10720*), showing fibrous fruit wall and seeds with curved, C-shaped embryos, ×3. **G-I,** Fruits of *Cornus* (Cornaceae). **G,** Longitudinal fracture showing typical ovoid shape and numerous silica-replaced resin bodies, IU 6274, ×5. **H,** Longitudinal fracture showing one of the septa and scattered resin bodies, IU 6273, ×5. **I,** Transverse section through the specimen in H, showing three single-seeded locules: plane of compression oriented vertically, ×9. Scale bars: A, B, 1 cm; C, I, 1 mm; D, E, G, H, 2 mm; F, 5 mm.
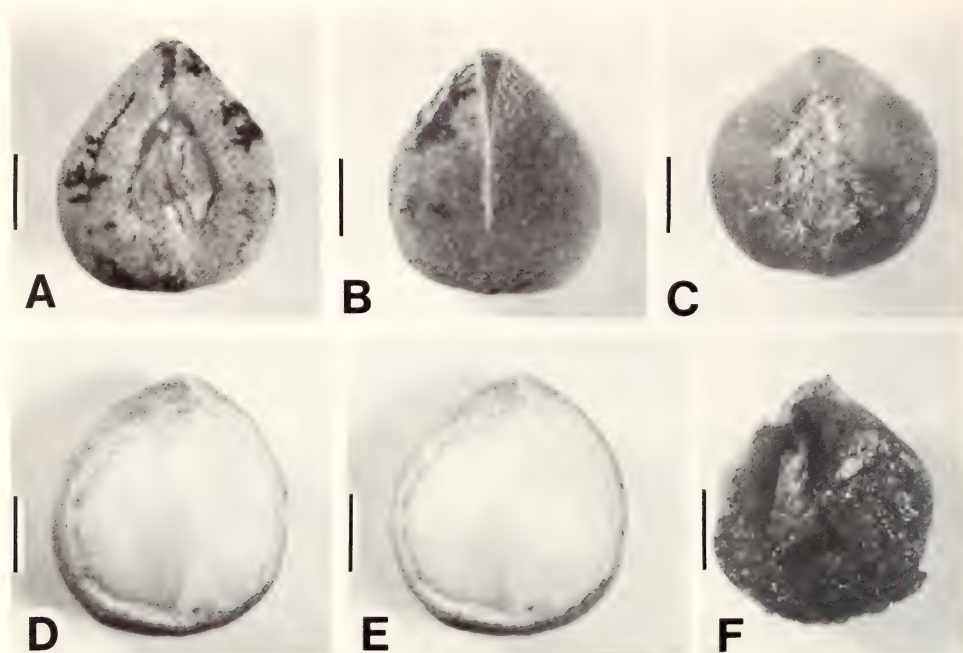
FIG. 21.   Fruits of fossil and extant Meliosmaceae. **A,** Fossil *Meliosma* endocarp showing ventral scar, IU 5970, ×5. **B,** Endocarp in A showing dorsal keel, ×5. **C,** Endocarp of extant *Meliosma alba* (Schlechtend.) Walp., ventral view, F184439, ×5. **D, E,** Fossil *Meliosma* endocarp fractured to show locule-cast; stereo-pair, IU 5971, ×5. **F,** Holotype of *Meliosma rostellata*, comb. nov. (*Carpites rostellatus* Lesquereux, 1878, pl. 60, figs. 12, 13); Golden, Colorado, USNM 503, ×5. Scale bars: A–F, 2 mm.

(1933) note that the fossil only differs from endocarps of *Cornus* in having more than two locules. However, in extant *Cornus* occasional fruits have more than two locules, and Eyde (1988) places *Dunstania* in synonymy with the extant genus.

Meliosmaceae

Meliosma rostellata (Lesquereux), comb. nov. (*Carpites rostellatus* Lesquereux, 1878, pl. 60, figs. 12, 13). Figure 21A,B,D–F.

Endocarps that are subglobose, 6.5–7.0 mm high, 6–7 mm broad, and 4.5–5.3 mm deep with a well-defined dorsal keel and a prominent funicular pore on the ventral face (fig. 21A,B,D,E). The endocarp surface is smooth and the thin wall encloses a single seed (fig. 21D,E).

Recognition of *Carpites rostellatus* Lesquereux as a species of *Meliosma,* and its occurrence in the Almont flora, extends the fossil record of *Meliosma* into the Paleocene and perhaps into the uppermost Cretaceous based on the material described by Lesquereux (1878). The type specimen of *C. rostellatus* (fig. 20F; USNM 503) is from the Denver Formation (Knowlton, 1930, p. 131) near Golden, Colorado, and therefore of uppermost Cretaceous or lowermost Paleocene age. Although not as well preserved, the type of *C. rostellatus* is identical in size and external morphology to the Almont material, and we assign them to the same species. Similar and probably conspecific endocarps also occur in the Paleocene Fort Union Formation near Hell's Half Acre, central Wyoming (IU loc. 15740). *Meliosma rostellata* is the earliest known occurrence of the family in the fossil record but subsequently the genus occurs in the Eocene of North America and the Early Tertiary of Europe (Van Beusekom, 1971).

The genus *Meliosma* comprises approximately 60 extant species divided between two subgenera (subgenus *Meliosma* and subgenus *Kingsboroughia* (Liebm.) Beus.; Van Beusekom, 1971) that occur in warm temperate regions in Asia and Central and South America. *M. rostellata* lacks the distinct marginal funicular canal characteristic of the living subgenus *Meliosma,* and the endocarps are therefore more similar to those of subgenus *Kingsboroughia,* for example, *M. alba* (Schlechtend.) Walp. (fig. 21C). Subgenus *Kingsboroughia* com-
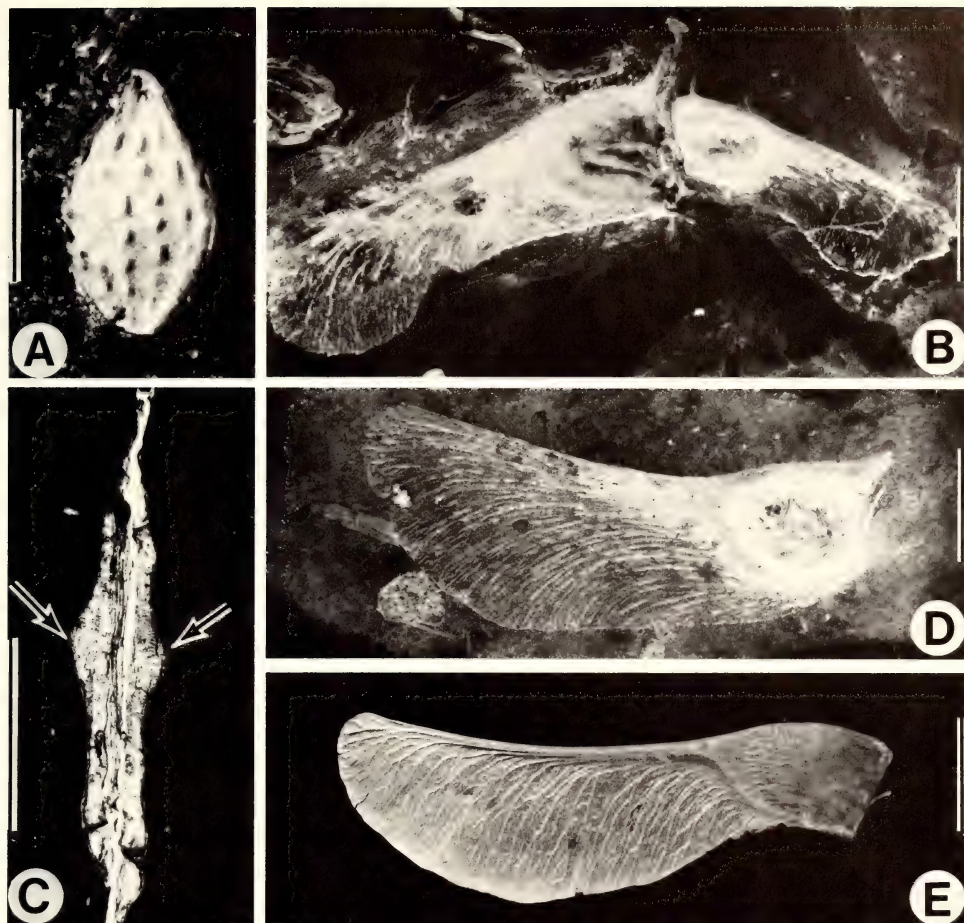
Fig. 22. Fossil fruit of Icacinaceae and miscellaneous fossil and extant angiosperm reproductive structures. **A,** *Palaeophytocrene* endocarp, pp33791, ×4.5. **B,** Schizocarp consisting of a pair of attached samaras, pp34206, ×1.5. **C,** Transverse section through the fruit body of fossil samara derived from a schizocarp showing two lateral ribs (arrows), pp34485, ×5. **D,** Single samara, iu 5972, ×1.5. **E,** Samara of extant *Acer platanoides* L., ×1.5. Scale bars: A, C, 5 mm; B, D, E, 1 cm.

prises three extant species disjunct between the mixed mesophytic forest of eastern Asia and the warm temperate forests of southern Mexico (Van Beusekom, 1971). *M. rostellata* is similar to *M. cantiensis* Reid & Chandler and *M. jenkinsii* Reid & Chandler from the Early Eocene London Clay Formation in southern England (Reid & Chandler, 1933) and to *M. gonnensis* from the upper Paleocene of Gonna near Sangerhausen, DDR (Mai, 1987). These species conform in endocarp morphology to subgenus *Kingsboroughia* (Van Beusekom, 1971). Endocarps referable to subgenus *Meliosma* are not recorded from the Paleocene of North America but are known in the Early Eocene London Clay Formation (Van Beusekom, 1971), the Paleocene of Gonna, DDR (Mai, 1987), and the Middle Eocene Clarno Formation of eastern

Oregon (Bones, 1979). Leaves or leaflets similar to those of *Meliosma* subgenus *Kingsboroughia* have not been recognized in the Almont assemblage. Leaves referred to *Meliosma flexuosa* (Hickey, 1977) are treated here as Platanaceae, type C foliage (fig. 13A,B).

Icacinaceae

Palaeophytocrene sp. Figure 22A.

Elliptical pitted endocarp that is 7 mm long, 4.5 mm wide, and about 1 mm thick in the compression. The exposed surface shows about 30 pits aligned in five longitudinal rows, indicating that a total of about 60 pits covered the surface of the endocarp (fig. 22A).

The Almont specimen resembles the fossil icaci-naceous genus *Palaeophytocrene* Reid & Chandler, which is known from several species in the Eocene of southern England (Reid & Chandler, 1933) and Oregon (Scott, 1954). The specimen is smaller than all previously described species. Similar endocarps have been described from the Fort Union Formation in Montana by Brown (1962, p. 91, pl. 67, fig. 26) as "impression of a seed showing pits arranged in longitudinal rows", and we have also recovered a single specimen from the Fort Union Formation at Hell's Half Acre, Wyoming (IU loc. 15740). Endocarps with similar pits are characteristic of extant genera in the tribe Phytocrenae of the Icacinaceae.

The Icacinaceae are a common element in many Early Tertiary floras (Reid & Chandler, 1933; Chandler, 1964; Collinson, 1983). Today they are a tropical family consisting of about 400 species of trees, shrubs, and lianes distributed among approximately 60 genera (Willis, 1973).

Miscellaneous Fossil Angiosperm Reproductive Structures

Schizocarpic Samara. Figure 22B–D.

Samaras that are 2.75–4.5 cm long and 0.9–1.5 cm broad (fig. 22B,D). The fruit body is basal, circular to elliptical in outline, 0.5–0.6 cm wide, and 2–3 mm thick with a prominent lateral longitudinal ridge on both surfaces (fig. 22C). The wing is elongate with a straight or convex heavily vascularized proximal margin and a rounded apex (fig. 22D). The distal margin may be more or less straight, or slightly concave basally, convex apically, and lacks a prominent sulcus. Veins in the wing diverge from the fruit body and the proximal margin toward the distal edge. The venation is fine and subparallel with frequent dichotomies and anastomoses. Basally the fruit is abruptly truncated by a prominent abscission scar more or less perpendicular to the proximal margin (fig. 22B,D). Most specimens also show a proximal keel representing the remains of a common stipe projecting from the basal edge of the fruit body (fig. 22D). One specimen shows a pair of attached fruits (fig. 22B), and it is clear that the plane of abscission that separated the fruits also divided the stipe. Remains of a perianth have not been observed.

The description given above follows the terminology of Wolfe and Tanai (1987). These large winged fruits appear to be the same species as that

figured as *Acer* sp. by Brown (1962, pl. 46, fig. 10) and Hickey (1977, pl. 37, fig. 7) from the Paleocene Fort Union Formation of central Wyoming and the Paleocene Bear Den Member, Golden Valley Formation of North Dakota. Although the fruits are very similar to those of extant *Acer* (e.g., fig. 22E) in general shape, venation, and presence of basal attachment scars, the stipitate condition of the fossil species is more pronounced than in extant species of *Acer* that we have examined. *Acer negundo* L. is one of the most similar species in having a short stipe above the perianth. One specimen from Almont shows a pair of basally attached samaras, but the possibility that the fruits were originally borne in threes (as in the related family Sapindaceae) cannot be excluded (cf. Wolfe & Tanai, 1987).

The extant genus *Acer* contains approximately 200 species, with the greatest diversity concentrated in China (Willis, 1973). The genus has an extensive fossil record (Walther, 1972; Friedrich & Simonarson, 1982; Tanai, 1983; Wolfe & Tanai, 1987). The earliest unequivocal leaves of *Acer* are recorded from the uppermost Paleocene of southeastern Alaska and the subsequent increase in the abundance and diversity of fossil fruits and foliage suggests that the major diversification of the genus occurred during the Eocene and Oligocene (Wolfe & Tanai, 1987). No obvious leaves of *Acer* have been recognized from Almont or other Fort Union localities, and those described as *A. silberlingi* Brown (1962) were excluded from the Aceraceae on the basis of several characters of venation by Wolfe and Tanai (1987, p. 210).

Nonschizocarpic Samara. Figure 23A–C.

Samaras that are approximately 3.5 cm long and 0.9 cm wide. Each fruit encloses a thick oval seed basally, 0.7–0.9 cm long, 0.5–0.6 cm wide, and 2.5–3.0 mm thick. Apically the fruit expands into a wing similar to that of *Acer* with fine, subparallel venation arising from the fruit body and the proximal margin, arching toward the distal edge, with occasional dichotomies and anastomoses (fig. 23A,C). The fruit body in several specimens shows a faint reticulate pattern of ridges. There is a distinct flap of tissue on the straight edge of the wing just apical to the fruit body (fig. 23A,C). Basally, the samaras are elongated into a distinct, more or less median, pedicel parallel with the longitudinal axis of the seed (fig. 23A,C).

Brown (1962, p. 91, pl. 67, figs. 6, 7) discussed

and illustrated samaras similar to the Almont specimens from the Fort Union Formation of central Montana, which he suggested may be related to Sapindaceae. A similar fruit from the Lower Oligocene flora of Florissant Colorado was tentatively assigned to this family as *Thouinia*(?) by MacGinitie (1953), but the sapindaceous samaras that we have examined, including *Thouinia* and *Thouinidium,* are borne either in pairs or in threes, and the isolated fruits usually show a prominent truncation of the seed body at the point of attachment. This feature does not occur in the Almont and Florissant specimens. Our material is also superficially similar to samaras of *Acer* but differs in the presence of a flap of tissue on the straight margin, the lack of a distinct proximal attachment scar, and the longitudinal rather than lateral orientation of the pedicel. Comparisons suggest a closer similarity to the extant genus *Securidaca* (Polygalaceae), which comprises approximately 80 species of tropical climbers (Willis, 1973). Fruits of extant *Securidaca* possess a distinct flap, or flange, of tissue on the straight margin of the wing and a thick reticulate fruit body (fig. 23D). In *Securidaca,* however, the remains of the perianth are usually preserved at the base of the fruit and this is not visible in any of the fossil specimens.

Elliptical Biwinged Fruit. Figure 23E.

Fruit consisting of an elliptical central body 6 mm long and 3 mm wide, longitudinally aligned, and centrally positioned within an elliptical lamina. The lamina is 20 mm long and 11 mm wide formed by two semi-elliptical wings (fig. 23E). Fruit borne at the apex of a slender pedicel 1.5 mm long that shows no evidence of persistent perianth parts. The fruit is retuse at the apex and cuneate at the base. A distinct longitudinal ridge separates the two wings and divides the fruit body in half, possibly indicating the presence of a bilocular ovary. The wings are thin with fine subparallel radiating veins.

A fruit similar to the Almont specimen is figured by Brown (1962, pl. 24, fig. 18) from the Paleocene of eastern Montana, and assigned to *Ulmus rhamnifolia* Ward. However, the Almont specimen differs from *Ulmus* in the lack of a distinct persistent perianth and the course of the median longitudinal ridge. In *Ulmus* only one of the two carpels develops and deflects the longitudinal ridge along the margin rather than along the center of the fruit body. Similarly, in the samaras of *Eucommia* (Eu-

commiaceae) the ridge on the outside of the unilocular ovary is deflected around the margin of the single seed that usually develops from the two ovules present at anthesis (Cronquist, 1981).

Fruit with Three Laterally Attached Wings. Figure 23 F–I.

Winged fruits with an elongated seed-bearing central body, 5–6 mm long, and three radially arranged vertical wings (fig. 23F,G,I). In transverse section (fig. 23H) the central body is unilocular, triangular with a wing borne on each angle, and shows no evidence of dehiscence. The wings are elliptical, 7–10 mm long, 4.5–6.0 mm wide, and gradually narrow apically and basally toward their point of attachment with the central body. Veins or fibers in the wings form a dense anastomosing network (fig. 23G). Fruits are usually exposed by a fracture plane that passes along two of the wings leaving the third only partially exposed (fig. 23F) or buried in the matrix. The three wings are clearly visible in transverse sections of reassembled specimens (fig. 23H). One specimen shows a slender peduncle 4 mm long (fig. 23I).

A similar fruit was figured by Brown (1962, pl. 24, fig. 17) from the Paleocene of central Wyoming and assigned to *Ulmus rhamnifolia* Ward. When only two of the three wings are exposed these fruits are superficially similar to *Ulmus,* but their triradiate structure and the lack of a pair of persistent styles excludes them from the Ulmaceae. Triwinged fruits of similar morphology occur in several modern families, including Sapindaceae, Rhamnaceae, and Zygophyllaceae, but in most cases such fruits are schizocarps that split into three parts at maturity. The fossil fruits resemble those of *Wimmeria* (fig. 23J,K) (Celastraceae) in retaining the three wings at maturity, the presence of a single locule, the shape and venation of the wings, and the presence of a slender pedicel without prominent scars. Pending more detailed anatomical comparison between the fossil and extant *Wimmeria* we have not assigned the fossil to this modern genus.

Pedicellate Capsule with Papillate Seeds. Figure 24A–E.

Ovoid capsules that are 10 mm long and 7 mm wide with an obtuse to rounded base and an acute apex (fig. 24A,B). Capsules occur either isolated,

36
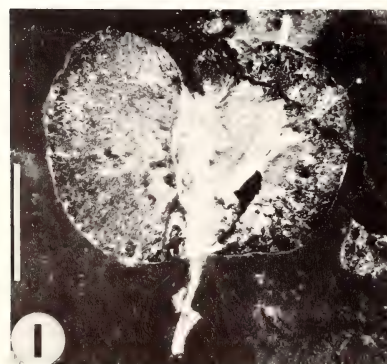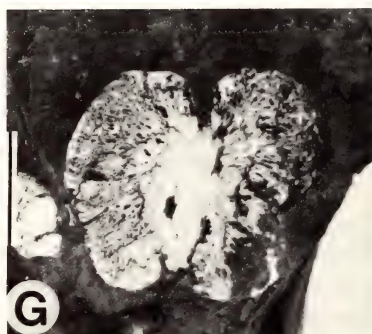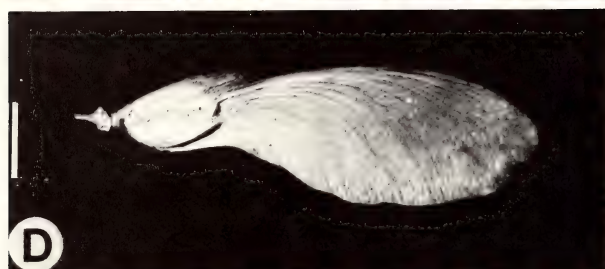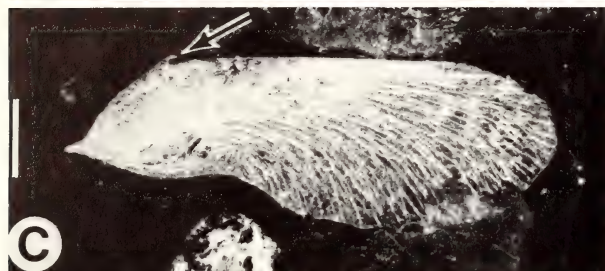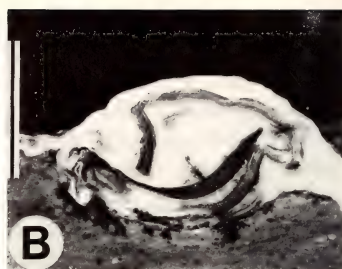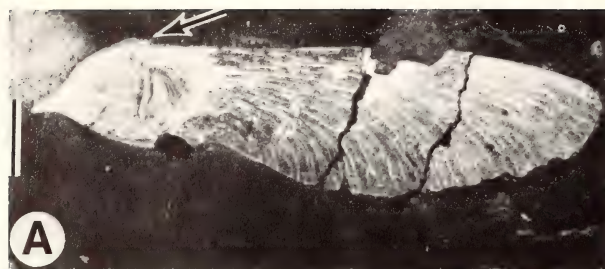
or attached to pedicels 5–8 mm long in a branched infructescence (possibly a cyme). The fruits have a solid central column and five radially arranged locules (fig. 24C). Seeds are elliptical, about 3 mm long, 1.5–2.0 mm wide, and have bulbous epidermal cells that form distinct papillae both internally and externally (fig. 24C–E). Broken fruits suggest that there were two seeds per locule but this needs to be confirmed by serial sectioning. Seeds are rarely found dispersed within the sediment (fig. 24E).

A similar pedicellate fruit is figured by Hickey (1977, pl. 54, fig. 6) as "ovoid fruits" from the Camels Butte Member (Eocene) of the Golden Valley Formation, North Dakota, and additional specimens have been recovered from the Fort Union Formation in Wyoming (IU loc. 15778 and 15740).

Head of Tricarpellate Fruits. Figure 24F–K.

Infructescences consisting of numerous tricarpellate fruits aggregated in an ovoid head 18–25 mm in diameter (fig. 24F,G). Fruits are obovate in longitudinal view (fig. 24H–J), rounded-triangular in cross section (fig. 24K), 9–12 mm long, and 4–6 mm in maximum width. Distally fruits taper to a persistent style, which is expanded at the apex (fig. 24I,J). Individual fruits, isolated from the infructescences, are very common. Each fruit contains three single-seeded locules approximately 7–9 mm long and 1–2 mm in diameter. The fruit wall consists of a fibrous endocarp 0.2–0.3 mm thick, surrounded by mesocarp 0.3–0.5 mm thick composed of isodiametric cells (fig. 24I–K). The mode of seed attachment is not known.

Fruits of this kind are abundant at several localities of the Fort Union Formation ranging from southern Wyoming (e.g., IU loc. 15778) to eastern Montana (USGS loc. 8519), although we are not aware of any previous descriptions in the literature. Except at Almont, the fruits are usually so compressed that their original morphology is difficult to interpret. At most localities, these fruits are associated with leaves of "*Viburnum*" *antiquum,* suggesting either that they occurred in similar ecological settings or that they were produced by the same species of plant.

Six- to Seven-Loculed Fibrous Fruit.
Figure 25A–C.

Ellipsoidal fruits that are 12–16 mm long and 8–10 mm wide. Fruits are elliptical in lateral outline with a length/width ratio of about 1.5, and hexagonal or heptagonal in cross section. Six to seven septa 0.3 mm wide radiate from a solid central column to delimit either six or seven (fig. 25C) locules. The external wall of the fruit is approximately as thick as the septa (fig. 25C). The folded remains of seed coats preserved within the locules indicate at least one large seed per locule. More detailed study is needed to determine the orientation, number, and placentation of ovules.

Lateral compressions of these fruits have been illustrated from other localities of the Fort Union Formation as *Viburnum tilioides* Ward (Ward, 1887, pl. 51, figs. 4–7; Brown, 1962, pl. 67, figs. 18, 19, 24, 25, 30, 31). However, the multilocular fibrous fruits of this fossil are clearly different from the single-seeded drupes with soft pericarp that are characteristic of extant *Viburnum.*

Fruit of 9 to 11 Single-Seeded Locules.
Figure 25D–F.

Multilocular fruits that are approximately 5 mm high and contain 9 to 11 single-seeded locules. The fruits are elliptical in transverse section and about 9 mm broad and 5 mm wide. The outermost layer does not have a definite cuticle, is probably not complete, and may represent the remains of the mesocarp. Internally there are 9–11 locules with

←

FIG. 23. Miscellaneous fossil and extant angiosperm reproductive structures. A, Nonschizocarpic fossil samara similar to that of extant *Securidaca* (Polygalaceae); note dorsal flap (arrow), PP34492, ×2. B, Section through body of fossil fruit showing fractured sclerenchyma layer in fruit wall, PP34562, ×6. C, Nonschizocarpic samara similar to that of extant *Securidaca*: note dorsal flap (arrow), PP34197, ×2. D, Samara of extant *Securidaca* sp., ×2. E, Fossil elliptical biwinged fruit; note medial vascular strand, PP34213, ×3. F, Fossil fruit with three laterally attached wings resembling extant *Wimmeria* (Celastraceae); note fragment of third wing (arrow), PP34189, ×3. G, Fossil fruit resembling extant *Wimmeria,* PP34515, ×3. H, Section through fruit in G with counterparts reassembled showing three wings, ×5. I, Fossil fruit resembling extant *Wimmeria* showing pedicel, IU 6185, ×3. J, Fruit of extant *Wimmeria pubescens* Radik, F1730569, ×3. K, Fruit in J viewed from above showing three wings, ×5. Scale bars: A, C–G, I, J, 5 mm; B, 3 mm; H, K, 2 mm.
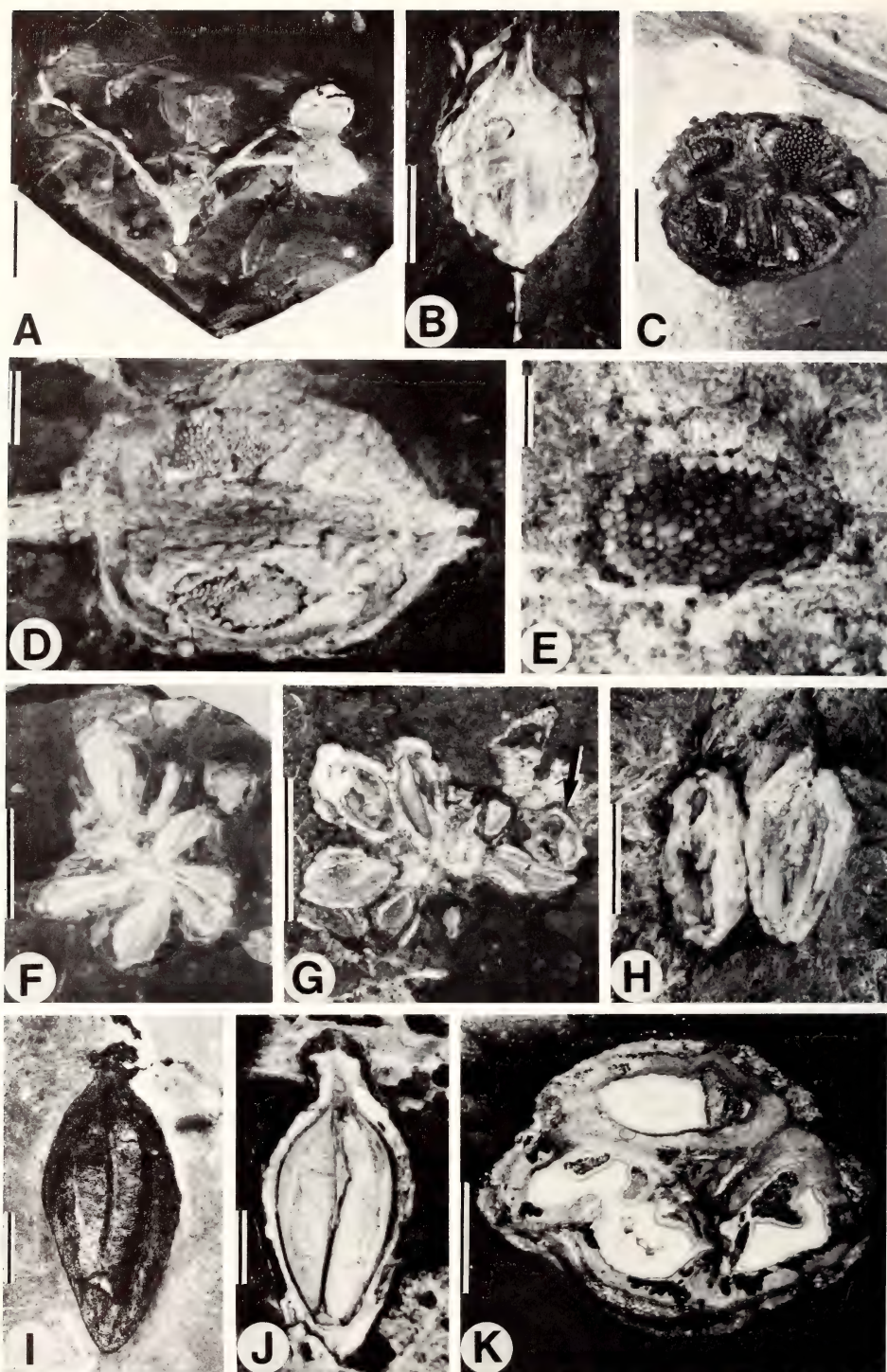
FIG. 24. Miscellaneous fossil angiosperm reproductive structures. **A-E,** Pedicellate capsule with papillate seeds. **A,** Portion of infructescence showing three attached capsules, IU 5979, ×1. **B,** Single capsule showing apices of capsule valves and possible remains of perianth, PP34474, ×2.7. **C,** Transverse section through a single carbonaceous capsule with five locules containing papillate seeds, PP34475, ×5. **D,** Longitudinal fracture through a capsule in A showing seeds with bulbous epidermal cells, ×5. **E,** Fracture through a dispersed seed showing casts of bulbous epidermal cells, PP34567, ×10. **F-K,** Heads of tricarpellate fruits. **F,** Infructescence with radiating tricarpellate fruits, PP34462,

long axes parallel to one another. Each locule is surrounded by a continuous layer of columnar cells 0.088 mm thick. The septa between the locules are formed by two adjacent layers of these columnar cells. Each locule contains a single obovoid seed that is rounded-triangular in cross section, basally rounded, but strongly pointed at the micropylar end. Seeds are about 3.5 mm long, 2.3 mm deep, and 1.2 mm wide, with an outer layer about 0.2 mm thick consisting of a spongy mass of ovoid cells. Cells internal to the spongy layer are quadrangular in surface view and aligned in longitudinal rows. The raphe runs through the spongy layer along the ventral angle of the seed. Internal tissues of the seeds are preserved in solid clear silica and readily separate from the fruit leaving most of the spongy layer adhering to the locule except around the raphe at the chalazal end where the spongy layer adheres more strongly to the inner tissues of the seed (fig. 25E).

We have not noted this type of fruit at any other North American locality. However, morphologically very similar fruits are recorded from the lower Eocene London Clay flora as *Carpolithus bowerbanki* Reid & Chandler (1933). The London Clay specimen differs from the Almont material only in its larger size.

Thick-Walled Unilocular Fruit. Figure 25G–I.

Ovoid thick-walled unilocular fruits that are 13–15 mm long and 7–10 mm deep and wide. The fruits are usually thinner in the plane of compression and show subrounded facets both in transverse sections and superficial fractures. The wall shows occasional fractures (fig. 25H), indicating at least some distortion during compression in the sediment. The wall is about 1.0–1.8 mm thick and consists of a mass of small equiaxial cells, 10–20 μm in diameter. About seven longitudinal vascular bundles about 0.4 mm in diameter are present in the fruit wall adjacent to the locule surface. A single seed with a thin testa occupies the locule.

We are unaware of descriptions of this fruit from other Paleocene localities, but specimens preserved as siltstone casts, and showing the resistant

vascular bundles, are present in collections from the Fort Union Formation of the Wind River Basin, central Wyoming (Signor Ridge, IU loc. 15757). The systematic relationships of this fruit remain to be determined.

Globose Fruit with Irregular Surface Pits. Figure 25J.

Unilocular fruits that are globose, 8–10 mm long, and 7–9 mm wide. Fruit wall consisting of a single homogeneous layer of more or less isodiametric cells. We interpret this layer as the remains of a hard endocarp from which the outer tissues have been lost. Endocarp with numerous irregular slit-like pits longitudinally oriented and scattered over the surface. Contents of the locule are poorly preserved but each apparently contained a single seed.

Although these fruits are rare at the Almont locality they are easily confused with poorly preserved sclerotestas of *Ginkgo* seeds. The lack of detailed information on these fruits precludes any consideration of their possible systematic relationships.

Six-Lobed Calyx. Figure 25K.

Calyx, 18 mm in diameter, consisting of six lobes. Each sepal is 5–6 mm long, 3–4 mm wide, apically pointed and lacks prominent venation. Sinuses between the sepals are acute.

Although only one specimen of this calyx was recovered from Almont, and preparation failed to reveal other floral organs, the general morphology is similar to flowers with six to seven sepals described from other Paleocene and Eocene localities of western North America that have stamens with *Pistillipollenites* pollen *in situ*. One such flower is figured by Hickey (1977, pl. 55, fig. 12), from the Golden Valley Formation, and another is described from the Eocene of Horsefly Mine, British Columbia, Canada (Stockey & Manchester, 1988; see also Crepet & Daghlian, 1981). The botanical affinities of these floral remains are still uncertain.

$\leftarrow$

×1.5. **G,** Infructescence with radiating tricarpellate fruits; note longitudinal fracture through a locule-cast and transverse section showing three locules (arrow), IU 5976, ×2. **H,** Longitudinal fracture through two dispersed fruits showing thick fruit wall, IU 5975, ×3. **I,** Dispersed fruit longitudinally fractured through the fruit wall and showing expanded apex of style, PP34487, ×5. **J,** Dispersed fruit longitudinally fractured along the surface of two locule-casts, PP34469, ×5. **K,** Transverse thin section through dispersed fruit showing three locules and anatomy of fruit wall, PP34467, ×7.5. Scale bars: A, F, G, 1 cm; B, H, 5 mm; C, D, I–K, 2 mm; E, 1 mm.
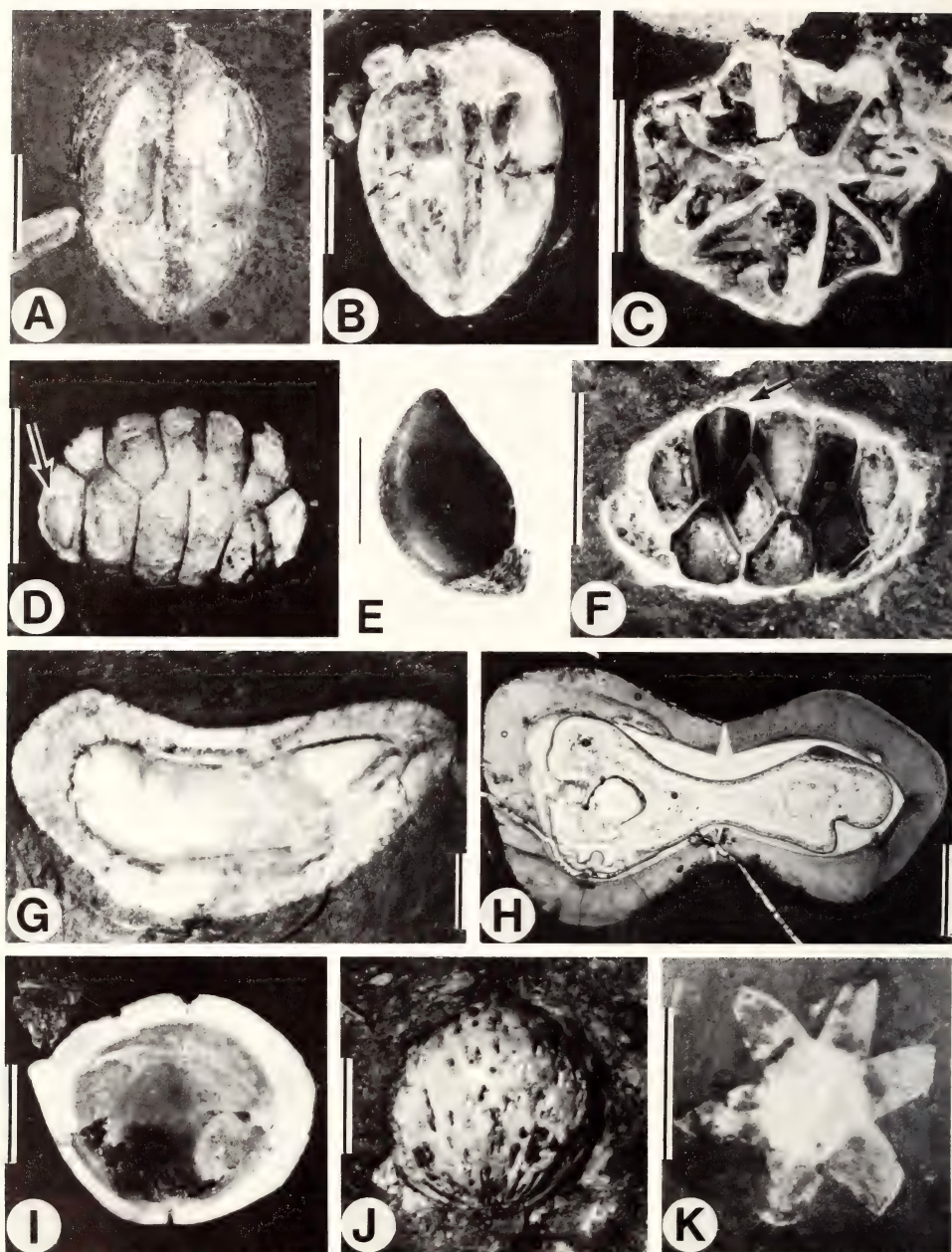
FIG. 25. Miscellaneous fossil angiosperm reproductive structures. **A–C,** Six- to seven-loculed fibrous fruit. **A,** Longitudinal fracture showing elliptical outline, PP34491, ×2.5. **B,** Oblique longitudinal fracture with fracture plane predominantly passing through septa separating the locules, PP34479, ×2.5. **C,** Transverse fracture showing angular outline and seven locules, PP34419, ×4. **D–F,** Fruit of 9 to 11 single-seeded locules. **D,** Transverse fracture through fruit apex showing arrangement of locules; note exposed seeds and position of the septa (arrow), PP34564, ×4. **E,** Single seed removed from fruit in F showing adhering cells of the spongy layer at base and smooth inner tissue, ×7. **F,** Transverse fracture showing thin septa, locules, and single seed *in situ* (arrow), PP34460, ×4. **G–I,** Thick-walled unilocular fruit. **G,** Longitudinal fracture showing thick wall and surface of locule-cast; note groove corresponding to one of the vascular bundles in the inner portion of the fruit wall, PP34510, ×5. **H,** Transverse section through fruit in G showing thick fruit wall and the testa of the single seed, ×6. **I,** Longitudinal fracture through rounded fruit, PP34493, ×2.5. **J,** Globose fruit with irregular surface pits, PP34513, ×2.5. **K,** Six-lobed calyx showing radiating sepals, UND 13060, ×2. Scale bars: A–D, F, I, J, 5 mm; E, G, H, 2 mm; K, 1 cm.

Fig. 26. Miscellaneous fossil angiosperm reproductive structures. **A–C,** Fruit with five to six concrescent follicles. **A,** Transverse fracture showing five unequally developed carpels, PP34480, ×4. **B,** Irregular longitudinal fracture showing three locules and a short apical style, IU 6265, ×4. **C,** Seed removed from locule, IU 6267, ×4. **D–F,** Clavate structure. **D,** Longitudinal fr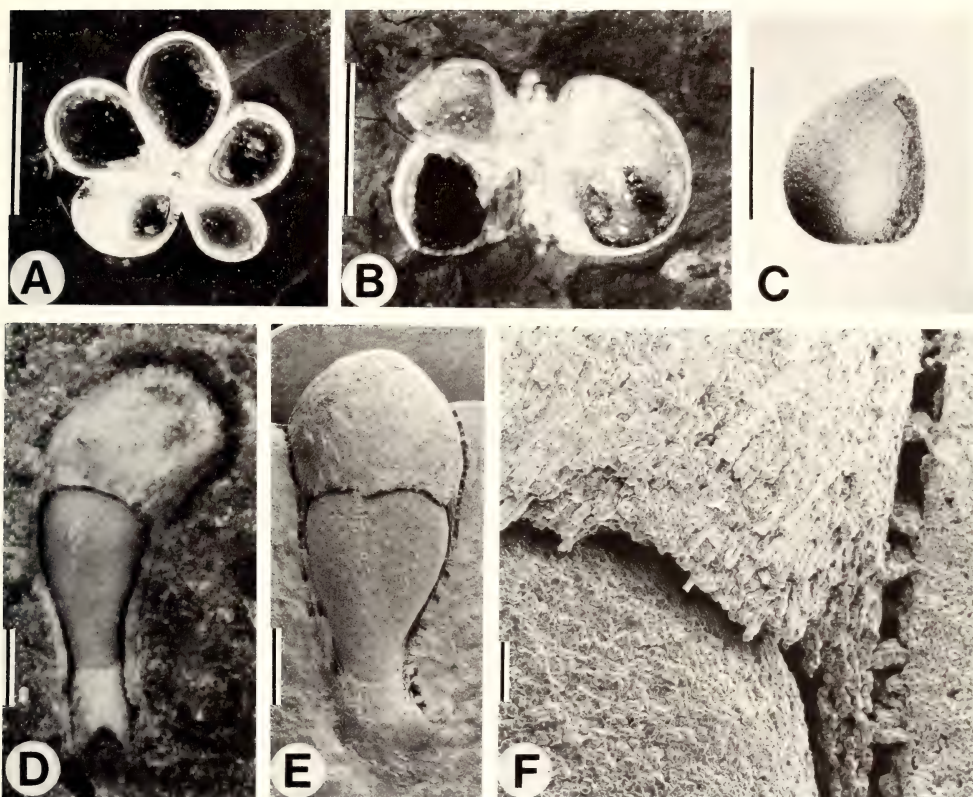acture showing general organization, IU 6269, ×10. **E,** Scanning electron micrograph of longitudinal fracture, IU 6270, ×10. **F,** Scanning electron micrograph showing cellular details of the terminal globose body in E, ×80. Scale bars: A–C, 5 mm; D, E, 1 mm; F, 100 μm.

Fruit with Five to Six Concrescent Follicles.
Figure 26A–C.

Compound fruits consisting of five to six radially arranged, single-seeded, ventrally concrescent follicles (fig. 26A). The follicles are ovoid, typically 6 mm long, 3–4 mm wide, 4–5 mm deep. They are rounded dorsally but constricted ventrally along the central axis of the compound fruit (fig. 26B). The fruit wall is 0.2–0.3 mm thick and smooth externally. Possible persistent styles terminate the central axis of the fruit (fig. 26B). Each follicle contains a single seed (fig. 26C).

This fruit is not known to occur at other localities. Most of the specimens are broken obliquely so that the number of follicles is unclear. Two specimens (e.g., fig. 26A) show five follicles and another (IU 6266) shows six, but the more typical number remains to be determined. Dispersed individual follicles are found occasionally, suggesting that the fruit may have separated into "mericarps" at maturity as in some Malvaceae and Sterculiaceae.

Clavate Structure. Figure 26D–F.

Small, club-shaped structures 4.0–5.5 mm long, borne on a stalk (possibly a pedicel) 1.0–1.5 mm long and 0.8 mm in diameter. The stalk articulates with a vase-shaped structure about 2 mm long that broadens apically to about 1.3 mm (fig. 26D,F). This, in turn, articulates with a terminal globose body about 2 mm in diameter. The entire clavate structure including the stalk is enveloped by a single outer layer of uniform cells about 80 μm thick.
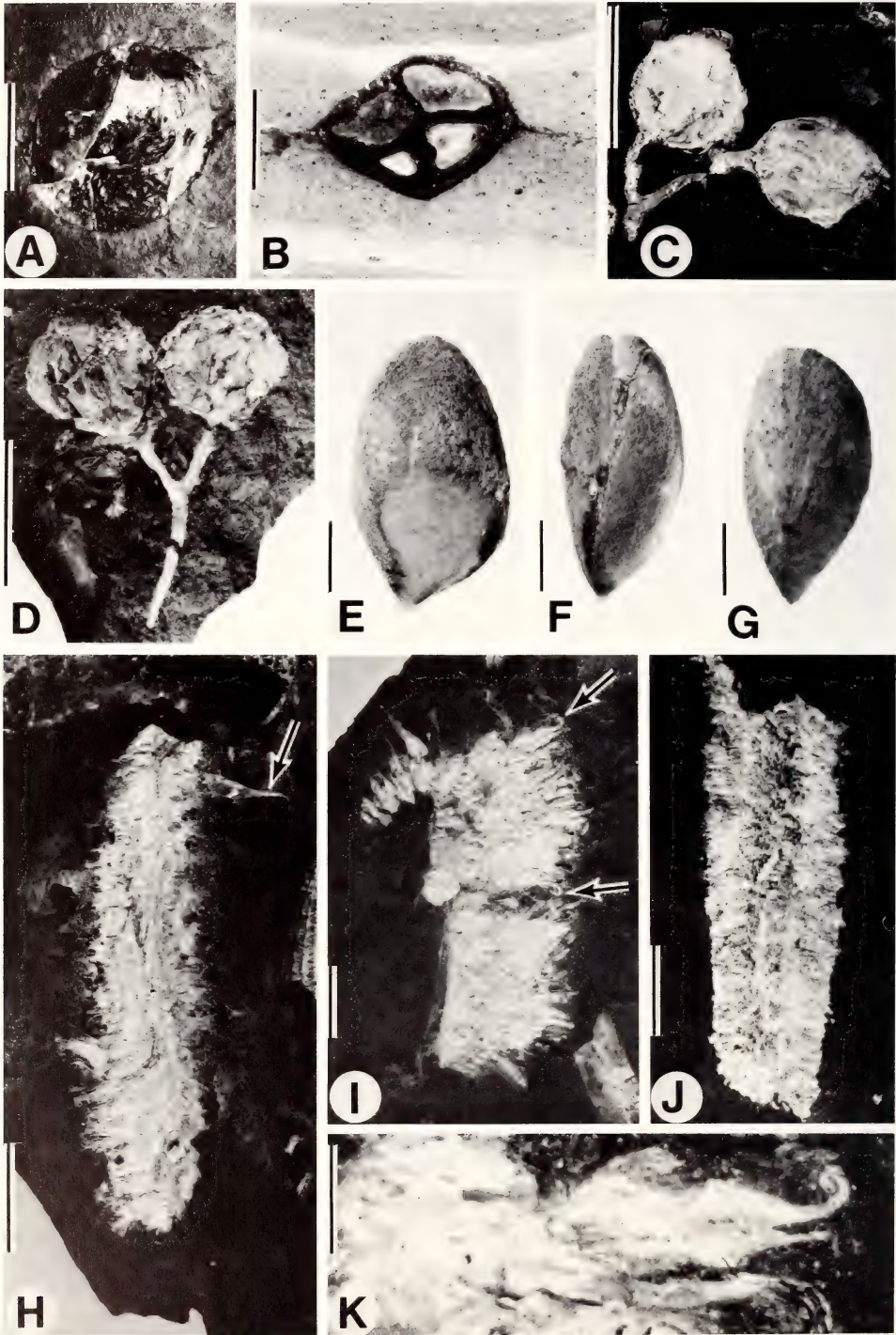
FIG. 27. Miscellaneous fossil angiosperm reproductive structures. **A,** Fleshy fruit, PP34511, ×3. **B,** Four-loculed winged fruit in transverse section, IU 6968, ×7. **C,** Two globose pedicellate capsules, PP34490, ×2. **D,** Two globose pedicellate capsules attached to a common stalk, IU 6963, ×2. **E-G,** Asymmetric ellipsoidal seeds. **E,** Lateral view, IU 6966, ×5. **F,** Dorsal view of seed in E, ×5. **G,** Dorsal view, IU 6967, ×5. **H-K,** Elongate infructescences. **H,** Infructescence with a single fruit attached (arrow), IU 6983, ×3. **I,** Broad infructescence showing numerous attached

The morphology of these structures is uncertain and their botanical affinities are unknown.

Fleshy Fruit. Figure 27A.

More or less spherical fruits that are typically about 1.0 cm in diameter, with a thick outer cuticle. Except for a distinct scar, about 0.3 mm in diameter, which is visible on several specimens, the outer surface is smooth. This scar may indicate the position of the style. Specimens are generally flattened on the bedding plane and distorted by compression.

These fruits superficially resemble the sarcotesta of seeds referred to *Ginkgo* (p. 6, fig. 2D–F) but lack the hard sclerotesta characteristic of that genus. The systematic affinities of these fossils are uncertain, although the thick outer cuticle and single style suggest the possibility of a relationship to extant Lauraceae.

Four-Loculed Winged Fruit. Figure 27B.

Fruit consisting of a central body 2.8–3.8 mm in diameter with a pair of thin longitudinal lateral wings, each at least 1.2 mm wide. The central body is rounded-quadrangular in cross section, with four locules separated by thick septa (fig. 27B).

This fruit is known from a single specimen exposed in a transverse fracture. Although it is distinct from the other fruits recorded from Almont, more detailed investigation involving serial sectioning and/or longitudinal fractures will be necessary to clarify its morphology and determine its systematic relationships.

Globose Pedicellate Capsule. Figure 27C,D.

Fruits that are spheroidal, 6–9 mm diameter, five-carpellate with a fibrous exterior and five fibrous septa radiating from a central column. Fruits are borne on pedicels 5–8 mm long, and dehiscence was apparently septicidal. Fibers of the septa are oriented horizontally while those of the fruit wall are mostly longitudinal. Seeds not observed.

These fruits superficially resemble those described as "pedicellate capsule with papillate seeds" (p. 38, fig. 24A–E), but are more rounded apically, lack the papillate seeds, and have thinner outer walls and septa.

Asymmetric Ellipsoidal Seed. Figure 27E–G.

Seeds that are 7.5 mm long, 4 mm broad, 3 mm wide, and taper to a point at one end. The surface (testa?) is made up of two layers about 0.1 mm thick. The inner layer is poorly preserved in clear silica; the outer layer is composed of longitudinally to diagonally oriented fibers.

These seeds may have been produced by the same plant as the hamamelidaceous infructescences described earlier (p. 23, fig. 15A–E). The distinct hilar scar characteristic of the seeds of many Hamamelidaceae is not clearly visible, but the size and shape of the seeds are consistent with a hamamelidaceous relationship. Additional specimens are needed for a more detailed evaluation of relationships.

Elongate Infructescence. Figure 27H–K.

Elongate infructescences, about 8 mm wide and at least 25 mm long, that consist of a straight axis about 1 mm in diameter surrounded by closely packed slender fruits. All of the specimens are broken at both ends so that their full length is unknown. Each fruit appears to be an achene with a single persistent style that is often recurved distally (fig. 27H,I,K). Details of bract and perianth placement have not been determined.

Similar specimens have not been described previously in the literature. The individual fruits of these elongate infructescences resemble the achenes of fossil Platanaceae (Manchester, 1986; Crane, 1989), and their dense packing bears a superficial similarity to the condition in both fossil and extant representatives of this family. However, the infructescences of all known Platanaceae are more

←

fruits, note recurved styles (arrows), IU 6964, ×3. **J,** Compact infructescence lacking fruits but with densely packed floral remains, PP34464, ×2.5. **K,** Detail of fruit from I showing recurved style tip, ×15. Scale bars: A, H, J, 5 mm; B, E–G, I, 2 mm; C, D, 1 cm; K, 1 mm.

or less globose, and the lack of detailed information on inflorescence and floral structure precludes a more positive determination.

Staminate Inflorescence with Tricolpate Pollen.
Figure 28A–C.

Slender staminate inflorescences, up to 4.5 cm long and 8 mm broad, that consist of numerous flowers borne helically around a central axis typically less than 1 mm in diameter (fig. 28A,B). Flowers are borne terminally on short side branches of the inflorescence axis that are typically 1–2 mm long. Floral structure is unclear but each flower is composed of at least four perianth parts or bracts. Pollen is prolate, tricolpate, approximately 15 μm in polar length, and 12 μm in equatorial diameter. The colpi extend for two-thirds to three-quarters the length of the grain (fig. 28C).

Fossil inflorescences of this type have not previously been reported from the fossil record. Their systematic position is uncertain, but the tricolpate reticulate pollen and unisexual inflorescence suggest a general relationship to the Hamamelidae. Silica casts of the inner surface of the sporopollenin wall show short irregular ridges (grooves in the wall) arising at right angles from the colpus margin. It is not known whether these were an original feature of the pollen (e.g., endocracks) or were produced by diagenetic processes.

Staminate Inflorescence with Monosulcate Pollen. Figure 28D–G.

Ellipsoidal inflorescence, 2.5 cm long, 9 mm wide, apparently consisting of numerous densely crowded flowers on a stout axis, but details of floral morphology are unclear. Elliptical anthers projecting from the margin of the inflorescence are approximately 1.5 mm long, 1 mm wide (fig. 28D),

and contain monosulcate reticulate pollen (fig. 28E,G). The equatorial diameter of the pollen is about 22 μm, the polar length about 15 μm. The exine sculpture is reticulate with lumina typically 2 μm in diameter. Muri are supported by numerous distinct columellae (fig. 28F).

Inflorescences of this type have not previously been recorded from Paleocene or other fossil localities. The *in situ* pollen is of the *Liliacidites* type and it seems likely that the inflorescence was produced by a monocotyledon. Clarification of the systematic relationships of these inflorescences will require additional material.

## Miscellaneous Fossil Angiosperm Leaves

A variety of leaves that occur at Almont have not yet been assigned positively to a modern family. The following brief descriptions and accompanying illustrations are provided to facilitate comparison with foliage from other Early Tertiary fossil floras. More detailed analyses of individual leaf types will be necessary to clarify their relationships with extant taxa.

Monocotyledonous Leaf Fragments. Figure 29A,B.

Leaves probably parallel-sided (length and width unknown). Leaves lack a thick midvein, venation consisting of numerous parallel longitudinal veins of approximately equal thickness spaced 0.2–0.4 mm apart. Perpendicular or slightly oblique cross-veins connect between adjacent longitudinal veins at intervals of 1–2 mm (fig. 29B).

The systematic relationships of these leaves are uncertain although they have previously been recorded in the Fort Union Formation (Brown, 1962) and Golden Valley Formation (Hickey, 1977) where they are often associated with fragments of large rhizomes. These leaves are rare at the Al-

→

FIG. 28. Fossil inflorescences with pollen *in situ*. **A**-**C**, Staminate inflorescence with tricolpate pollen. **A**, Staminate catkin, PP33623, ×2.5. **B**, Staminate catkin showing floral parts in several orientations (arrows), PP33622, ×2. **C**, Scanning electron micrograph of pollen from specimen in B (IU stub 1704); note that pollen is triaperturate and preserved as internal casts and external molds, ×1,000. **D**-**G**, Staminate inflorescence with monosulcate pollen. **D**, Inflorescence showing anthers (arrows), PP34190, ×2.5. **E**, Scanning electron micrograph of pollen from specimen in D; note that pollen is monosulcate and preserved as internal casts and external molds, ×500. **F**, Scanning electron micrograph showing detail of pollen grain external mold; note the reticulate arrangement formed by the cavities indicating the position of columellae, and the absence of a distinct cavity attributable to a tectum, ×4,000. **G**, Scanning electron micrograph showing detail of internal cast of a pollen grain; note the groove formed by the single sulcus and depressions formed by inward bulges of the pollen wall in the lumina of the reticulum, ×2,125. Scale bars: A, B, D, 5 mm; C, G, 10 μm; E, 50 μm; F, 5 μm.
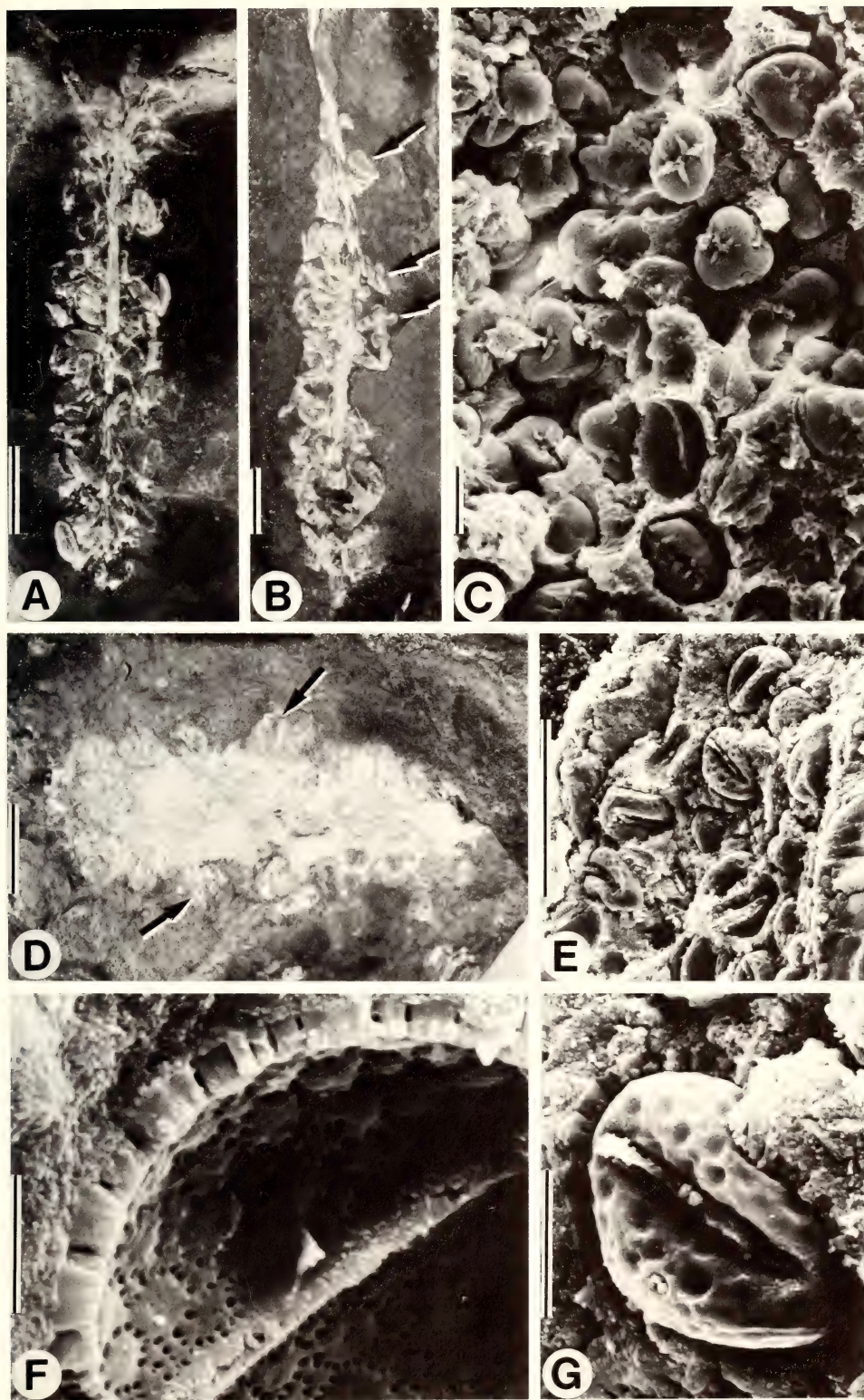
mont locality and rhizomes have not been recognized.

Porosia verrucosa (Lesquereux) Hickey.
Figure 29C,D.

Reniform leaves up to 1.0 cm long, 1.3 cm wide, and about 1 mm thick frequently occur in pairs (fig. 29C), and often have an apparent attachment scar in the center of the straight or slightly concave margin. Leaf margin often distinctly thickened (fig. 29D). The lamina has a characteristic rugulate texture, and occasional specimens show faint traces of reticulate venation.

These leaves are apparently the floating foliage of an aquatic plant and are common in many Paleocene floras (Bell, 1949; Brown, 1962; Chandrasekharam, 1974; Krassilov, 1976). Specimens from the Fort Union Formation were assigned to *Hydromystria expansa* (Heer) Hantke (Hydrocharitaceae) by Brown (1962). Hickey (1977) reassigned this material and that from the Golden Valley Formation to the fossil genus *Porosia* Hickey, which he included in the Araceae. Similar specimens also occur in the Late Cretaceous of North America (Hickey, 1977) and in the Maastrichtian–Danian of Amur in the far eastern USSR (*Limnobiophyllum scutatum* (Dawson) Krassilov, 1973b, p. 110, pl. 23, figs. 49–61). Krassilov (1973b) described and illustrated stomata from the Amur material as "bordered by 8–12 cells from which 2 are polar subsidiary cells and the rest encircling cells". Based on cuticular structure, Krassilov ruled out an affinity with Hydrocharitaceae, Lemnaceae, and Nymphaeaceae, and suggested a relationship to Araceae although no extant genus of the family has leaves identical to *P. verrucosa*.

Lacunate Leaf. Figure 29E–G.

Reniform to roughly circular leaves, about 1.3 cm long, 1.8 cm wide, and about 1 mm thick. Leaf margin thickened and the lamina consisting of two layers of numerous, closely spaced, more or less spherical, lacunae about 0.3–0.5 mm in diameter that are filled with silica in the fossil. The two layers of lacunae are separated by a continuous homogeneous layer of small more or less isodiametric cells.

The "punctate structure" described by Hickey (1977) from the Camels Butte Member of the Golden Valley Formation may be a similar lacunate leaf. Further work may demonstrate that this material is conspecific with *Porosia verrucosa* (Lesquereux) Hickey, but the specimens currently available differ from the *Porosia* leaves at Almont in their larger size and very prominent lacunae.

"Viburnum" antiquum (Newberry) Hollick.
Figure 30.

Leaf with an elliptical to ovate lamina, 2–14 cm long, 2–11 cm wide, with a length/width ratio of 1.0–1.9. Leaf apex typically rounded or obtuse (fig. 30B). Leaf base obtuse, rounded to cordate, and petioles usually more than one-third as long as the lamina (fig. 30A,B,E). Except in some small leaves (fig. 30E), the margin is serrate, with prominent, widely spaced, typically obtuse teeth that are best developed toward the leaf apex (fig. 30A–D). Venation pinnate with conspicuously branched craspedodromous secondary veins and prominent, percurrent tertiary veins.

Leaves designated *"Viburnum"* antiquum (Newberry) Hollick occur at many localities in the Fort Union Formation (Brown, 1962). They are often difficult to distinguish from those assigned to *"Viburnum"* cupanioides (Newberry) Brown but most Almont specimens have a broadly elliptical or ovate lamina similar to the majority of leaves included in *"V."* antiquum by Brown (1962). Similar leaves are illustrated as *Viburniphyllum finale* (Ward) Krassilov from the Paleocene of Amur (Krassilov, 1976, pl. 41, figs. 1–7). Although these fossils share some features with leaves of certain extant *Viburnum* species (Caprifoliaceae), the petioles are much longer and more robust than in the extant genus (fig. 30A,E). There is some similarity to leaves of certain Hamamelidaceae (e.g., *Hamamelis, Parrotia*) but the systematic relationships of this common Early Tertiary leaf type remain uncertain. This leaf type co-occurs at Almont and at other North American Paleocene localities with the heads of trilocular fruits described earlier (p. 38, fig. 24F–K) (Manchester, unpubl. obs.).

Averrhoites affinis (Newberry) Hickey.
Figure 31.

Leaf compound, imparipinnate, with a rachis up to 12 cm long and at least 6 pairs of subsessile leaflets. Leaflets have an elliptical lamina 6–12 cm long (mean 8 cm), 2.2–6 cm wide (mean 3 cm), with a length/width ratio of 1.8–2.5. Leaflet apex
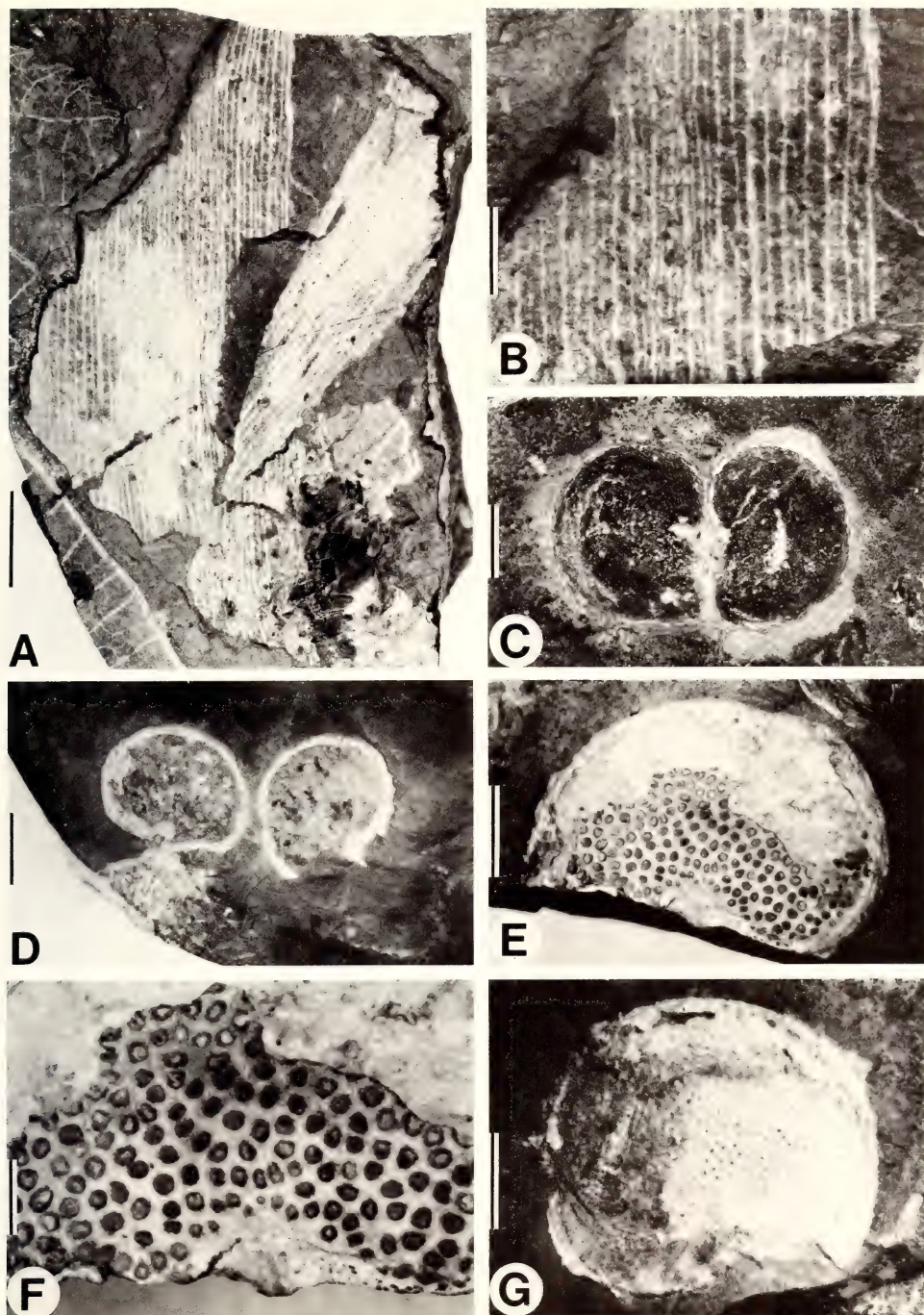
FIG. 29. Miscellaneous fossil angiosperm leaves. **A, B,** Fragments of monocotyledon foliage. **A,** Fragment of broad monocotyledonous leaf, IU 6776, ×2.5. **B,** Detail of venation from A showing cross-veins, ×6. **C, D,** *Porosia verrucosa* (Lesquereux) Hickey. **C,** Pair of attached reniform leaves showing characteristic surface texture, PP34483, ×2. **D,** Fragments of three leaves with prominent marginal thickenings, IU 6175, ×2. **E-G,** Lacunate leaf. **E,** Specimen showing distribution of lacunae, IU 6176, ×2.5. **F,** Detail of lacunae from E, ×5. **G,** Fracture along surface of a lacunate leaf, PP34481, ×2.5. Scale bars: A, C–E, G, 5 mm; B, F, 2 mm.
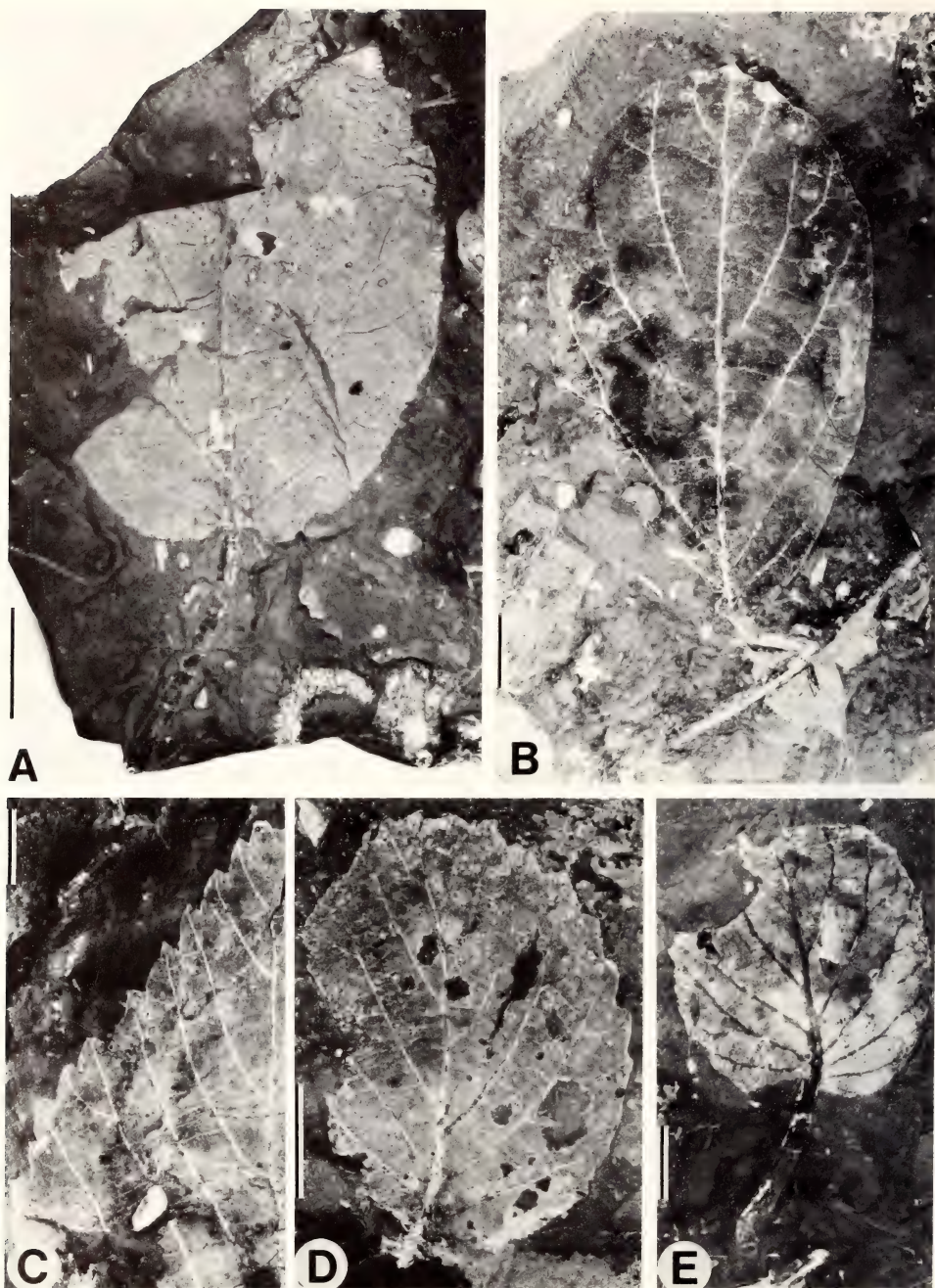
Fig. 30. Fossil leaves of "*Viburnum*" *antiquum* (Newberry) Hollick. **A,** Leaf showing long petiole and variable development of marginal teeth, ιυ 5974, ×0.75. **B,** Leaf with a predominantly entire margin and a few weakly developed teeth distally; note thin, branched, percurrent tertiary venation, pp34482, ×1. **C,** Detail of margin from leaf with well-developed teeth; note prominent craspedodromous secondary veins, percurrent tertiary veins, and sparse secondary teeth, pp34472, ×1. **D,** Broadly ovate leaf showing major venation and margin, ιυ 6962, ×0.75. **E,** Small, broadly elliptical leaf showing long thick petiole, major venation, and weakly developed teeth, pp34473, ×1. Scale bars: A, D, 2 cm; B, C, E, 1 cm.
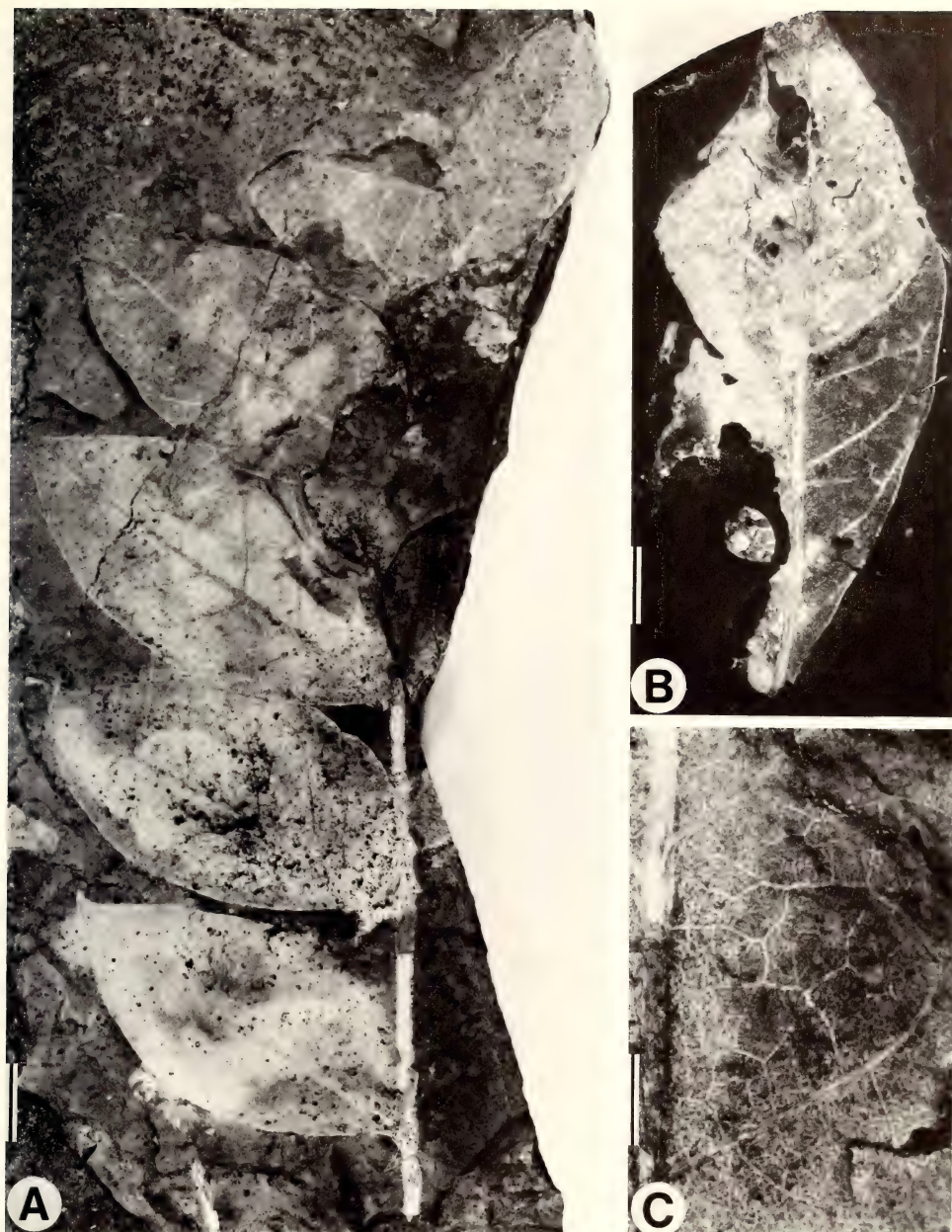
Fig. 31. Fossil leaves of *Averrhoites affinis* (Newberry) Hickey. **A,** Compound leaf with six attached leaflets, UND 13059, ×1. **B,** Single leaflet, PP34420, ×1. **C,** Detail of leaflet showing fine venation adjacent to midrib, PP34461, ×6. Scale bars: A, B, 1 cm; C, 2 mm.

acute, base obtuse to rounded, margin entire. Petiolules very short, 1–3 mm long. Lamina distinctly asymmetric and more extensively developed on the adaxial side. Venation pinnate, with approximately seven pairs of camptodromous alternate secondary veins that loop to join the supra-adjacent secondaries close to the margin (fig. 31B). Tertiary and higher order veins form irregular po-

lygonal areolae (fig. 31C), and the leaf often has a thin but distinctive marginal thickening (fig. 31B).

Leaflets usually occur isolated but are sometimes found attached to the rachis. The most complete specimen (fig. 31A) shows a rachis with 6 attached leaflets, from which at least 11 leaflets may be inferred. This species occurs at numerous localities in the Fort Union Formation (Brown,

1962) and Golden Valley Formation (Hickey, 1977). Specimens from the Fort Union Formation have previously been assigned to *Sapindus affinis* Newberry (Brown), and Krassilov (1976, pl. 42, figs. 1–5) illustrates similar leaves from the Paleocene of Amur as *Diplophyllum amurense* Krassilov. Hickey (1977) discusses the relationships of this foliage and points out certain similarities to leaves of Oxalidaceae.

Leaf Type I. Figure 32.

Leaf with an ovate, elliptical to circular lamina 5.5–12.0 cm long and 3.2–12.0 cm wide. Length/width ratio commonly about 1.7 in elliptical leaves, but sometimes as low as 1. Lamina symmetric or asymmetric. Leaf apex and base typically acuminate (fig. 32A,C), margin entire. Petiole frequently up to 2 cm long. Venation pinnate with camptodromous secondary veins forming loops well within the margin (fig. 32A). Tertiary and quaternary veins form numerous well-developed, transversely elongated loops between the secondary loops and the margin (fig. 32A). Intersecondary veins common. Tertiary veins percurrent, sinuous, and generally oriented perpendicular to the midvein. Quaternary and quinternary veins prominent and forming irregularly oriented four- to five-sided areoles with freely-ending sixth-order veinlets (fig. 32B).

These leaves are distinctive with excellently preserved higher order venation. Although relatively common at Almont, they have not been recognized at other localities in the Fort Union Formation. Krassilov (1976) describes similar leaves as *Nyssa bureica* Krassilov from the Paleocene of Amur.

Leaf Type II. Figure 33A–C.

Leaf or leaflet with an ovate, slightly asymmetric lamina 5.5–8.5 cm long, 3–5 cm wide, with a length/width ratio of 1.7–1.8 (fig. 33A). Leaf apex obtuse, base broad and rounded, margin entire. Petiole or petiolule short and stout, without transverse striations (fig. 33C). Venation pinnate with camptodromous secondary veins. Secondary veins are crowded near the leaf base and arise from the midvein at wider angles than those above (fig. 33A,C). Tertiary veins irregularly percurrent, 3–5 mm apart, but higher order venation is poorly preserved (fig. 33B).

These specimens have a broadened petiole or petiolule and venation similar to that seen in many extant genera of Leguminosae. However, transverse striations found on the petiolules of many extant legume leaflets are not seen in the Almont material.

Leaf Type III. Figure 33D,E.

Leaf with an elliptical lamina 14 cm long, 6 cm wide, and a length/width ratio of 2.3. Leaf apex acute to acuminate, base unknown. Venation pinnate, with camptodromous secondary veins. Leaf margin weakly serrate, with small, frequently inconspicuous, circular glands at the end of tertiary veins that arise from the loops of the secondaries (fig. 33E). Intercostal tertiaries percurrent, straight, and perpendicular to the secondary veins.

These leaves closely resemble specimens assigned to *Ternstroemites aureavallis* Hickey from the Early Eocene Camels Butte Member of the Golden Valley Formation that are thought to be related to extant Celastraceae or Theaceae (Hickey, 1977).

Leaf Type IV. Figure 33F.

Leaf apparently ovate, but with base missing, apex acute. Leaf margin mostly entire but minutely erose close to the apex. Venation acrodromous with a primary vein of moderate thickness and at least three pairs of well developed secondary veins that are strongly and uniformly curved toward the apex. Mode of origin of secondary veins unknown, but arising only in the lower two-thirds of the lamina. Innermost secondary veins extending almost to the leaf apex. Tertiary veins thin, widely spaced, percurrent, and more or less perpendicular to the midvein. Quaternary and higher order venation thin, poorly preserved.

This leaf type is represented only by a single incomplete specimen, but in the observable characters it closely resembles Paleocene leaves assigned to *Cornus hyperborea* Heer from the Bear Den Member of the Golden Valley Formation of North Dakota (Hickey, 1977), and from the Fort Union Group of Wyoming (Brown, 1962). More material is needed to fully characterize the Almont foliage and confirm the generic determination, but the presence of *Cornus* in the flora is unequivocally demonstrated by the presence of fruits (p. 31, fig. 20G–I).
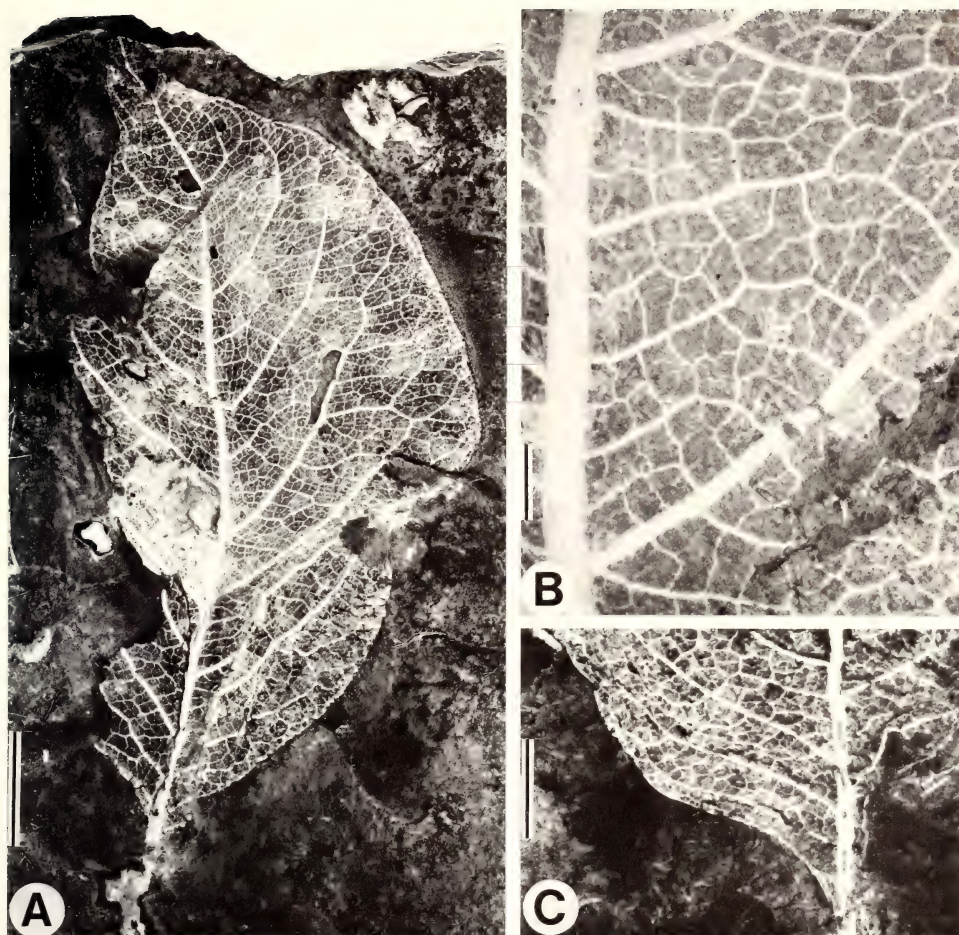
FIG. 32. Miscellaneous fossil angiosperm leaves, type I. A-C, Leaf type I. A, Leaf with asymmetric lamina and acuminate apex, PP34192, ×1.5. B, Detail of intercostal venation, PP34188, ×5. C, Detail of venation at leaf base, PP34199, ×1.3. Scale bars: A, C, 1 cm; B, 2 mm.

Leaf Type V. Figure 34A,B.

Leaf with a narrowly elliptical to obovate lamina, 8 cm long, 3 cm wide, and a length/width ratio of 2.7 (fig. 34A). Leaf apex acute, base obtuse with a petiole up to 5 mm long. Leaf margin entire. Venation acrodromous, suprabasal (fig. 34B), with a pair of strong secondary veins extending distally for more than three-quarters of the leaf length (fig. 34A). A fine intramarginal vein extends from the base of the lamina almost to the leaf apex (fig. 34B). Tertiary veins very thin, percurrent, and oriented approximately perpendicular to the midvein.

This leaf closely resembles the foliage of extant Lauraceae in having suprabasal acrodromy, an intramarginal vein, and percurrent tertiaries. However, leaf architectural patterns within this family overlap considerably among genera, and it is not possible to place this species in a modern genus with the information currently available. Only one specimen is known from Almont, but we have recovered comparable narrow lauraceous leaves from other localities in the Fort Union Formation. Ward (1887, p. 48, pl. 24, fig. 2) described similar material as *Cinnamomum lanceolatum* (Unger) Heer from Hodges Pass, Wyoming (?Upper Cretaceous).

Leaf Type VI. Figure 34C.

Large leaf with a slightly obovate lamina approximately 9 cm long, 7 cm wide, and a length/width ratio of about 1.3. Lamina slightly asymmetrical. Leaf apex obtuse, base cordate, and the
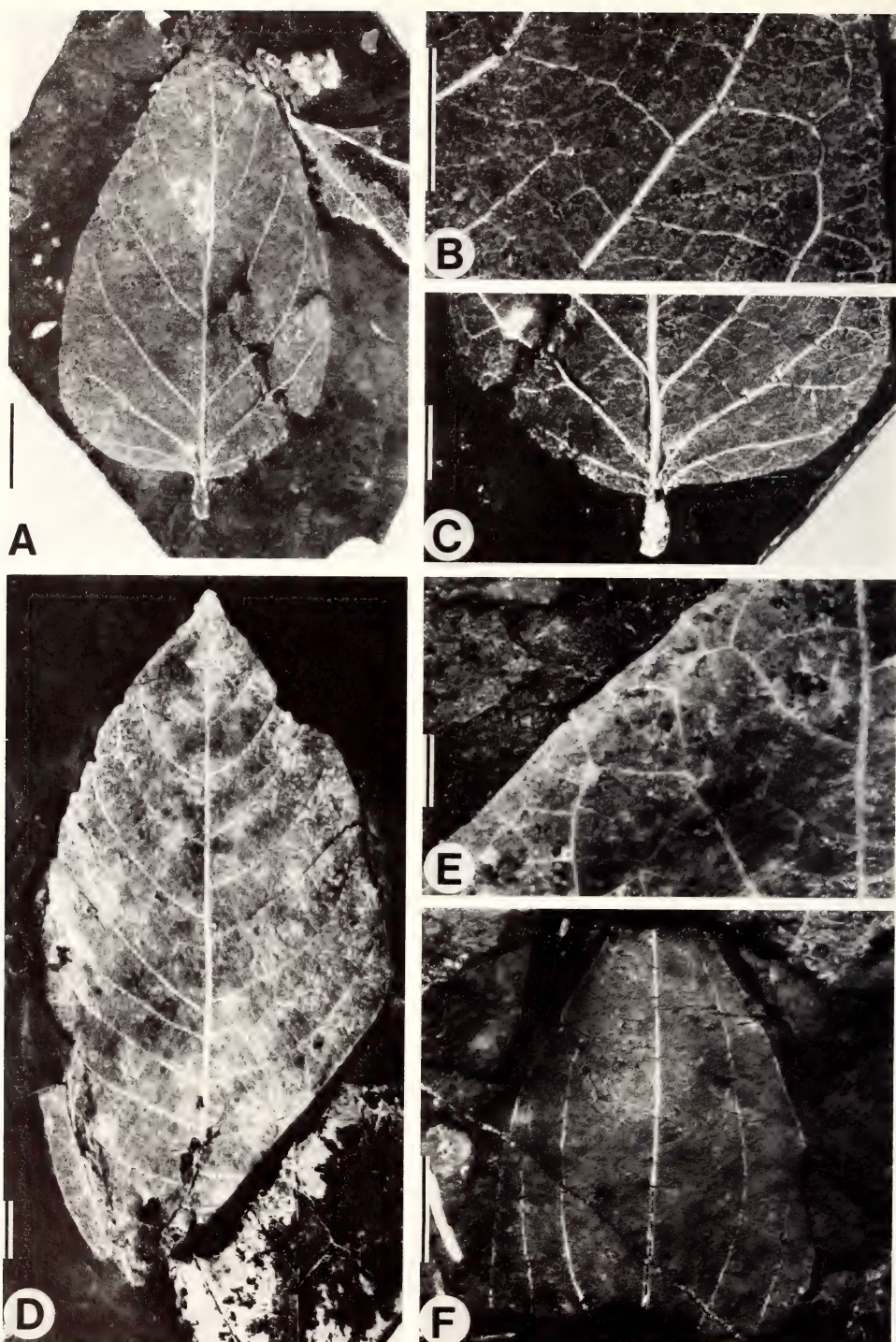
FIG. 33. Miscellaneous fossil angiosperm leaves, types II, III, and IV. A–C, Leaf type II. A, Ovate leaf showing asymmetric lamina and short petiole or petiolule, IU 5973, × 1.2. B, Detail of intercostal venation from counterpart of A, ×4. C, Detail of petiole or petiolule and venation at base of leaf from counterpart of A, ×2. D, E, Leaf type III. D, Leaf showing outline, entire margin, and major venation, PP34426, ×0.8. E, Detail of margin near leaf apex showing glands and marginal venation, PP34418, ×5. F, Leaf type IV showing entire margin and major venation, PP34471, ×1.5. Scale bars: A, D, F, 1 cm; B, C, 5 mm; E, 2 mm.
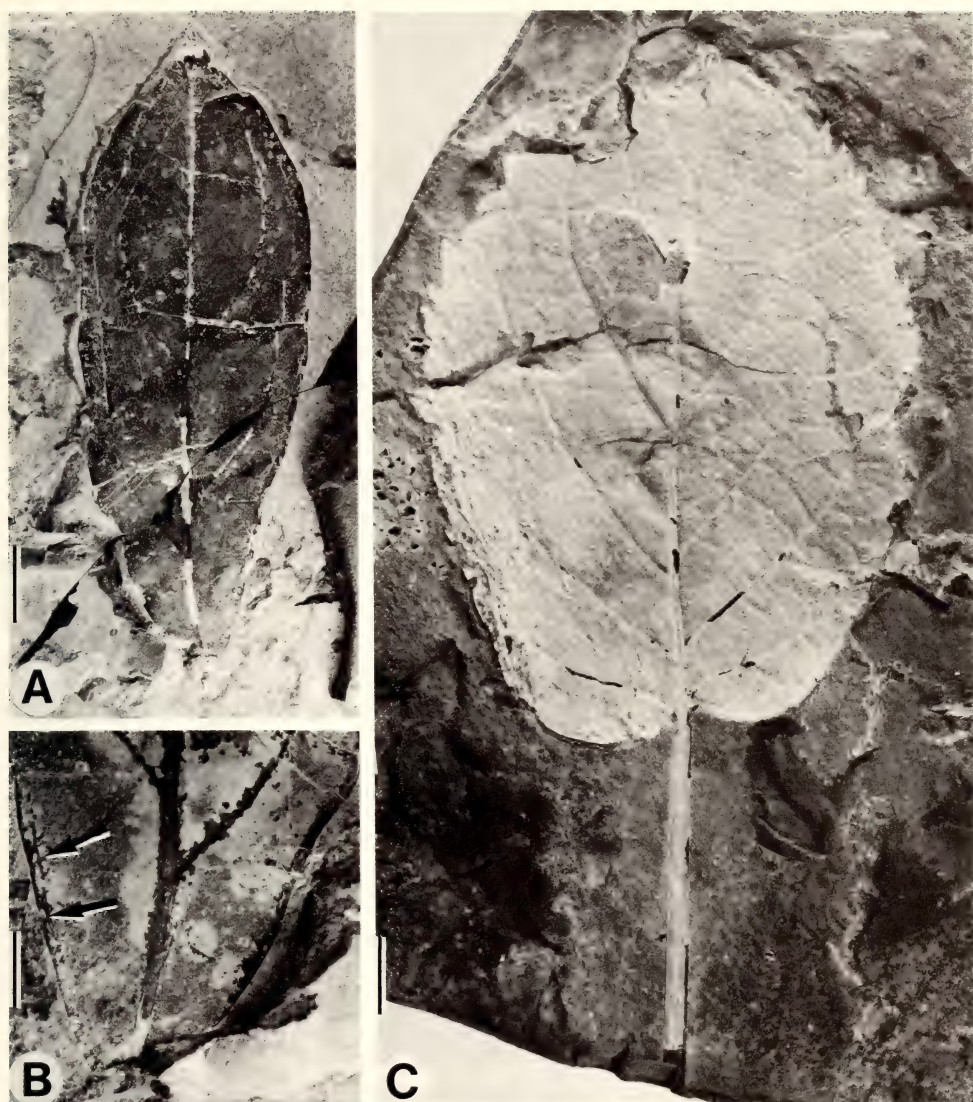
FIG. 34. Miscellaneous fossil angiosperm leaves, types V and VI. **A, B,** Leaf type V. **A,** Obovate leaf showing entire margin and major venation, IU 6180, ×1. **B,** Detail of leaf base from counterpart of A, showing fine intramarginal vein (arrows), ×2. **C,** Leaf type VI showing leaf outline, major venation, cordate base, and long petiole; note camptodromous secondary venation and acute teeth, IU 6183, ×1. Scale bars: A, C, 1 cm; B, 5 mm.

margin serrate. Petiole at least 4.6 cm long (fig. 34C). Venation pinnate, semicraspedodromous, with prominent marginal teeth supplied by tertiary veins. Secondary and tertiary veins forming loops within the margin. Lowermost pair of secondary veins arising from the base of the midvein at a wider angle than the more distal secondary veins. Tertiary veins prominent, usually straight or slightly convex, percurrent, and oriented perpendicular to the secondaries.

In general form this leaf resembles "*Viburnum*" *antiquum,* but has more acute, more closely spaced

teeth and does not show prominent, forked craspedodromous secondary veins. Leaves of this kind were illustrated by Brown (1962, pl. 44, figs. 1, 4, 6) as *Eucommia serrata* (Newberry) Brown, although some of the other specimens attributed to this species differ in having closely spaced teeth and closely spaced percurrent tertiaries. Leaves of extant *Eucommia* differ from the fossil in having an acute-cuneate leaf base, more irregularly percurrent tertiary veins, and irregularly oriented areoles. Chandrasekharam (1974) assigned leaves of this type from the Paleocene of southern Alberta

to *Tapiscia serrata* (Newberry) Chandrasekharam (Staphyleaceae). We have not recovered the distinctive fruits of *Tapiscia* from Almont or other Paleocene localities, although they occur in Eocene floras from both Europe (Mai, 1980) and North America (Manchester, 1988). The relationships of leaf type VI, whether to *Eucommia, Tapiscia,* or other taxa, remain uncertain.

Leaf Type VII. Figure 35A,B.

Large leaf with an ovate lamina 14 cm long, 9 cm wide, and a length/width ratio of about 1.7 (fig. 35A). Leaf apex obtuse, base acute. Leaf margin slightly crenulate distally (fig. 35B), entire proximally. Petiole at least 2 cm long. Venation acrodromous, basal, with craspedodromous secondaries. Basal pair of secondary veins well developed, extending about two-thirds of the distance to the leaf apex before terminating at the margin. Lamina constricted above the point of divergence of the basal secondary veins such that the veins form the margin at the extreme leaf base (fig. 35A). All secondary veins terminate at the tip of a marginal crenation (fig. 35B). Strong abmedial tertiary veins arise from the basal pair of secondary veins and also terminate at the margin. Tertiary veins percurrent, straight, uniformly spaced, and perpendicular to the secondaries.

Fossil leaves similar to leaf type VII were not recognized by Brown (1962) from the Fort Union Formation although Ward (1887) illustrates a superficially similar leaf type as *Cinnamomum affine* Lesquereux. The illustrations of *C. affine* however show camptodromous rather than craspedodromous venation.

Leaf Type VIII. Figure 35C,D.

Ovate leaves usually with an asymmetric lamina 3–5 cm long (possibly up to 12 cm), 1.0–4.2 cm wide, and a length/width ratio of about 2–3 (fig. 35C). Apical portion of lamina acute but with a rounded apex. Leaf base rounded to truncate. Leaf margin entire. Petiole very slender, up to 7 mm

long (fig. 35D). Venation is pinnate with about six pairs of widely spaced camptodromous secondary veins curving upwards inside the margin, and forming a system of marginal loops with peripheral tertiary veins. Tertiary veins between the secondaries, and those derived directly from the midrib, forming irregular polygonal areolae.

As far as we are aware, leaves of this type have not been recognized from other Early Tertiary fossil plant localities in the Rocky Mountain Region. They are readily distinguished from other leaves in the flora by their relatively small ovate lamina and thin petiole.

**Leaf Type IX. Figure 35E,F.**

Leaf with an ovate, symmetrical lamina 5.5–13.0 cm long, 3.5–7.0 cm wide, and a length/width ratio of about 2. Leaf apex obtuse, base acute and decurrent down the petiole. Leaf margin entire (fig. 35F). Petiole up to 11 mm long (fig. 35E). Venation pinnate with 8–10 camptodromous secondary veins forming clearly defined loops well within the margin. Tertiary veins straight and percurrent (fig. 35F). Quaternary and higher order veins delimit polygonal areolae but are poorly preserved in our material.

Leaves of this type are similar to some of the forms previously assigned to *Nyssa alata* (Ward) Brown (Brown, 1962). Details of morphology and venation are very like those of some extant *Psidium* species and these leaves may have been produced by the same species as the fossil fruits assigned to this genus (p. 31, fig. 20A–E).

Leaf Type X. Figure 36A,B.

Ovate leaf with a symmetrical lamina, about 9 cm long, 6.5 cm wide, and a length/width ratio of 1.4. Leaf apex not preserved; leaf base broadly rounded and slightly cordate. Leaf margin entire. Petiole at least 2 cm long (fig. 36A). Venation pinnate, camptodromous, with a straight midvein and about eight pairs of secondary veins. Basal pair of secondary veins arising from the midvein at a wider

→

FIG. 35. Miscellaneous fossil angiosperm leaves, types VII, VIII, and IX. **A, B,** Leaf type VII. **A,** Specimen showing characteristic form of the leaf base and widely spaced craspedodromous secondary veins, IU 6181, ×1. **B,** Detail of leaf margin from A, ×2.5. **C, D,** Leaf type VIII. **C,** Ovate leaf showing entire margin and thin petiole, IU 6268, ×1. **D,** Detail of leaf base from C showing margin and fine venation, ×2. **E, F,** Leaf type IX. **E,** Elliptical leaf showing obtuse apex, major venation, decurrent leaf base, and short petiole, PP34198, ×1.5. **F,** Detail of margin and intercostal venation from E, ×3. Scale bars: A, C, E, 1 cm; B, D, F, 5 mm.
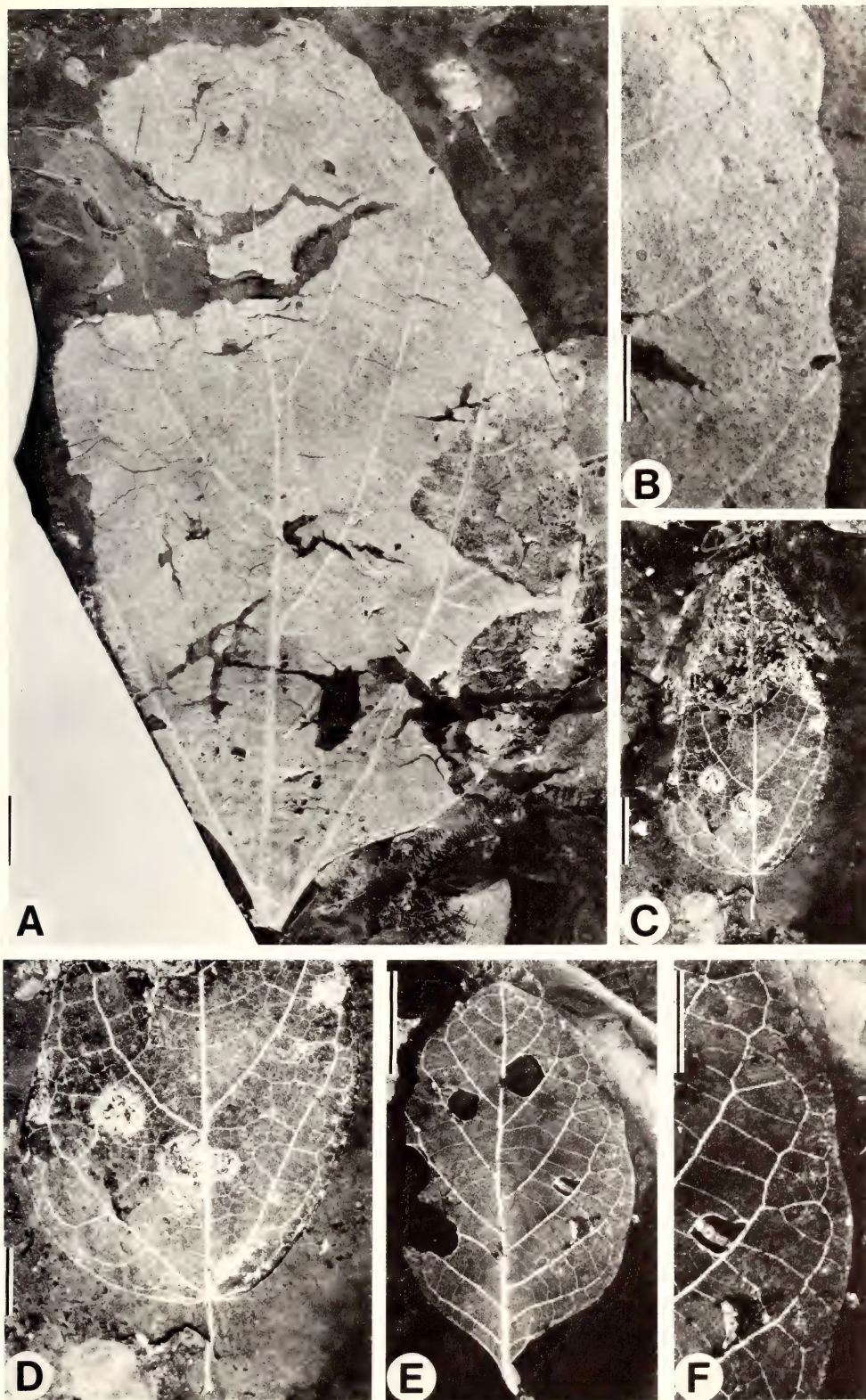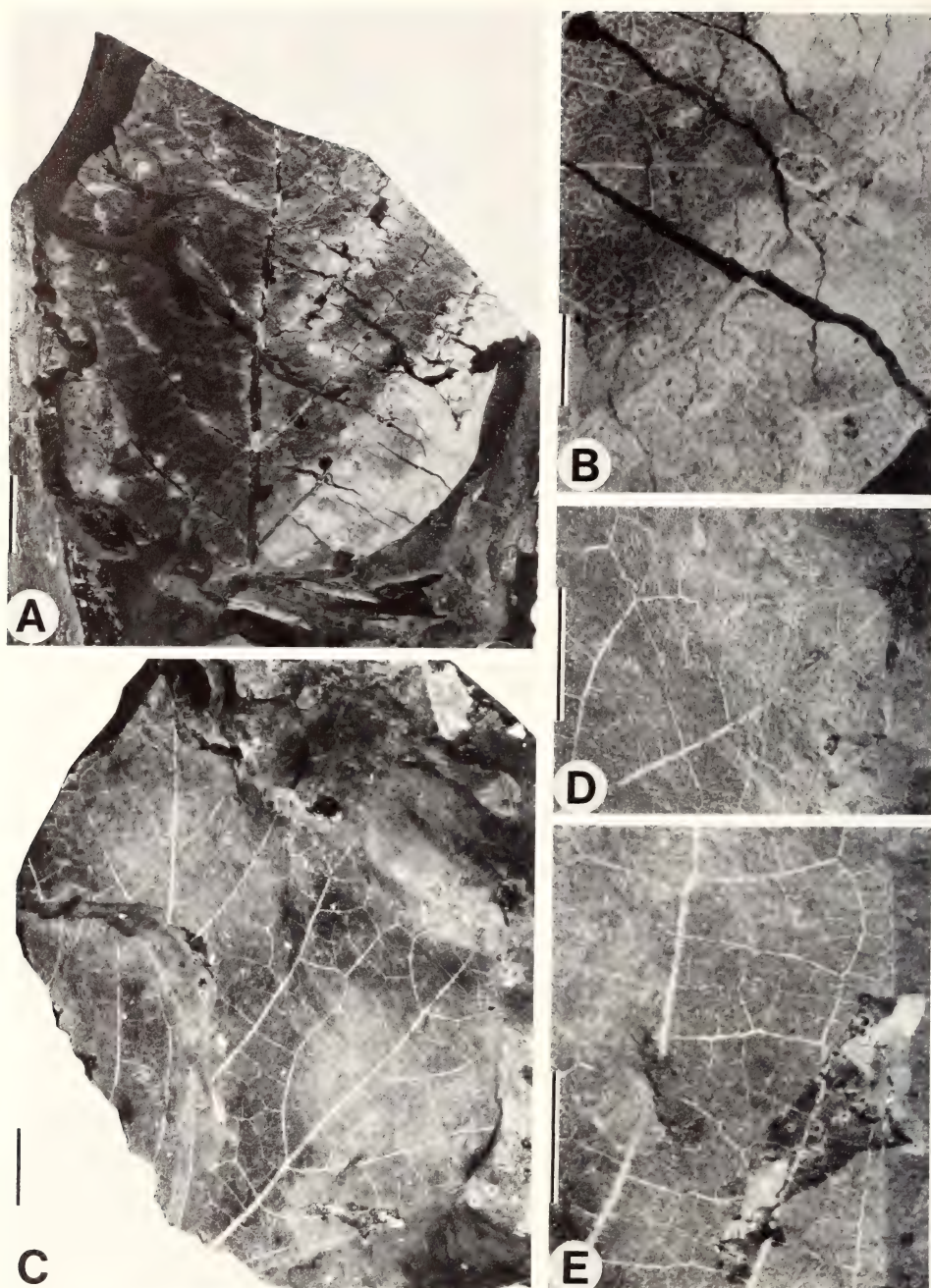
Fig. 36. Miscellaneous fossil angiosperm leaves, types X and XI. **A, B,** Leaf type X. **A,** Basal fragment of an entire margined leaf showing major venation, ɪᴜ 6178, ×1. **B,** Detail of higher order intercostal venation from A, ×6. **C-E,** Leaf type XI. **C,** Trilobed leaf showing outline and major venation; note left hand portion of lamina folded over the midrib, ɪᴜ 6182, ×1. **D,** Detail of apex of right leaf lobe in C, ×3.5. **E,** Detail of marginal venation from C, ×3.5. Scale bars: A, C, 1 cm; B, 2 mm; D, E, 5 mm.

angle than those above, and the two most basal pairs of secondaries are more closely spaced on the midrib than those above. A fine vein forms the leaf margin (fig. 36B). Tertiary veins percur-

rent, straight, perpendicular to the midvein, and forming loops inside the margin. Quaternary and higher order veins very fine, forming irregularly oriented polygonal areolae with once to twice

branched, curved veinlets (fig. 36B). Quaternary veins connect between the tertiary marginal loops and the marginal vein.

This leaf may be referable to the Menispermaceae (cf. p. 10, fig. 5). The manner in which the quaternary veins connect with the marginal vein, and the fine areolation are similar to that in extant Menispermaceae such as *Cissampelos*. Although the major venation is pinnate, the closely spaced secondaries near the leaf base suggest a possible origin from an originally actinodromous arrangement.

Leaf Type XI. Figure 36C–E.

Leaf with a broadly ovate, shallowly three-lobed lamina, about 8 cm long, 9 cm wide, with a length/width ratio of about 1. Leaf apex acute, base not preserved but probably obtuse or cordate. Margin predominantly entire, but poorly preserved and with indications of occasional teeth. Venation probably actinodromous but origin of the three primary veins not seen. Primary veins diverging at angles of about 45° and terminating in the three primary lobes (fig. 36C,D). Each primary vein producing five or six pinnate secondary veins, some of which form camptodromous loops while others apparently terminate in teeth. Tertiary veins percurrent between the secondaries, forming prominent camptodromous loops toward the margin (fig. 36C,E). Quaternary and higher order venation delimiting variously arranged polygonal areolae. Leaf surface distinctly pitted, perhaps indicating the presence of numerous hairs.

Leaf type XI may be a further variant of the three kinds of platanoid foliage from Almont. Better preserved material is needed to examine this possibility in more detail.

General Discussion and Conclusions

The taxa present in the Almont flora (Table 1) include many plants characteristic of middle to high latitude floras in the Paleocene of the Northern Hemisphere. In particular, there are many elements in common with the extensive Paleocene flora described from the Rocky Mountains and Great Plains of North America (Brown, 1962). We have recognized 30 different types of fruits and seeds, 6 different kinds of inflorescences and flowers, and 24 different kinds of leaves, which probably represent as many as 30 to 45 biological species depending on the extent to which the same species are represented by different isolated organs. Of the 515 Paleocene localities in North America from which Brown (1962) records plant fossils, only 17 yielded 10 or more species, and only 1 yielded more than 20 species (Hamer-Crane, pers. comm.). Taken together, the mean number of species per locality is less than three. Other Paleocene plant assemblages are equally depauperate. Wolfe (1966) recorded 24 angiosperms in the Paleocene Chickaloon flora of Alaska from eight localities. Hickey (1980) surveyed 66 localities in the Fort Union Formation (Group) of the Clarks Fork Basin in Montana and Wyoming and found an average of 9–12 species and a maximum of 25 at each locality. Similarly, the Paleocene flora of southeastern Amur, described by Krassilov (1976), consists of 56 species collected from 23 localities. The number of species at individual localities varies from 2 to 17 and only four localities have 12 or more species.

The number of species from Almont is much higher than is typical of individual Paleocene assemblages and this probably reflects both the intensity of collecting activity and quality of preservation compared to most other localities of this age. The Almont plant assemblage thus complements the more inclusive surveys of regional Paleocene floras from North America provided by Brown (1962) and Hickey (1977) from the Fort Union Formation and the Bear Den Member of the Golden Valley Formation, respectively, in providing improved insight into the plant community present at one time and in one place. In addition, while previous studies of Paleocene floras have focused primarily on leaf remains, the Almont plant assemblage provides important complementary information on associated reproductive structures.

The most abundant remains at the Almont locality are leaves of *Ginkgo,* leaves and achenes of *Nordenskioldia,* leaves and reproductive structures of *Palaeocarpinus,* and fruits of *Cyclocarya* (Table 1). Taxodiaceous remains are also common but the leafy shoots are generally damaged, suggesting the possibility of some transport. In contrast to many Paleocene floras, vegetative and reproductive material of *Platanus* and the *Joffrea/Nyssidium* complex is relatively rare. In the Fort Union Formation as a whole (Brown, 1962) cercidiphylloid and platanoid leaves are the most widespread elements in the flora, occurring at 12.8% and 9.5%, respectively, of the 515 localities

for which data are available (Brown, 1962). In the Paleocene flora of Amur the most widespread elements are *Taxodium olriki* (Heer) Brown and *Trochodendroides arctica* (Heer) Berry (Krassilov, 1976), while in the Clarks Forks Basin the "overall dominants" of the flora are *Cercidiphyllum genetrix* (Newberry) Hickey and the two conifers *Metasequoia occidentalis* (Newberry) Chaney and *Glyptostrobus europaeus* (Brongniart) Heer (Hickey, 1980).

Taphonomically the Almont assemblage presents several interesting features. The abundance of relatively delicate reproductive structures (e.g., staminate inflorescences), the large number of relatively complete leaves, and the general quality of preservation do not suggest vigorous transport of most of the plant material prior to deposition. The high diversity, in combination with the large number of winged fruits and seeds, is characteristic of lacustrine depositional environments (Spicer & Greer, 1986). Variation in the size, shape, and density of the plant parts indicates different hydrodynamic properties and suggests that sorting effects are relatively minor. The most interesting anomaly is the abundance of *Cyclocarya* fruits, which are clearly over-represented relative to other organs of the parent plant. *Cyclocarya* leaflets are only occasionally encountered at Almont and staminate catkins have not yet been recognized in the plant assemblage. The *Cyclocarya* fruits are not obviously damaged, the wing is usually well preserved, and they show no evidence of long distance transport. The absence of dispersed platanaceous fruitlets in the Almont collections is also unusual in view of the presence of staminate inflorescences and three kinds of platanaceous leaves.

Current knowledge of the Almont flora provides only a coarse estimate of paleoclimate, but nevertheless suggests that the flora reflects equable warm-temperate conditions. Although the taxodiaceous foliage may have been evergreen, *Ginkgo* and most of the dicotyledons that dominate the Almont assemblage, such as Betulaceae, Cercidiphyllaceae, Juglandaceae, Platanaceae, and perhaps "*Cocculus*", appear to have been deciduous, suggesting a seasonal climate. Few, if any, of the species appear to be broad-leaved evergreens, and cf. *Parataxodium* is the only conifer. These features, along with the moderate floral diversity, suggest vegetation physiognomically similar to that described for the present-day mixed mesophytic forest of Asia and the Atlantic coastal plain of eastern North America (Chu & Cooper, 1950; Wang, 1961; Dolph & Dilcher, 1979; Wolfe, 1979). In addition, many of the species in the Almont assemblage are referable to, or are related to genera that are represented in the modern mixed mesophytic forest.

The proportion of entire-margined dicotyledonous leaves at the Almont locality is 45% (9 out of 20) and 80% of the leaves are large *sensu* Dilcher (1973) (4 microphyllous; 11 notophyllous; 5 mesophyllous). The percentage of entire-margined leaves is higher than is typical for the mixed mesophytic forest of China but lower than would be expected in a tropical or paratropical forest (Wolfe, 1979). The percentage obtained for the Almont assemblage is close to that plotted by Dolph and Dilcher (1979) for parts of the mixed mesophytic forest in the piedmont of North and South Carolina. For the area near High Point, North Carolina, which is in the zone of 40–45% entire-margined leaves and 80% large leaves, the mean daily temperature for the coldest month is 4.5° C (averaging 10° C and −2° C for the warmest and coldest days), while the mean daily temperature for the warmest month is 24° C. There is an average of about 74 days a year in which the temperature is below 0° C, and the mean annual temperature is 15° C.

Similar temperature estimates have been made from other Paleocene floras in western North America. In the Clarkforkian (Upper Paleocene–Lower Eocene) of Clarks Fork Basin, Montana and Wyoming, Hickey (1980) obtained a value of about 40% entire-margined dicotyledonous leaves from a total of 70 species, and suggested a generally humid and temperate climate with a mean annual temperature of 13.5° C, and a mean annual range of temperature of 20° C. In the Upper Paleocene Bear Den Member of the Golden Valley Formation, Hickey (1977) calculated the percentage of entire-margined species at 30% in a total flora of 26 species. Based on this percentage and the distribution of extant relatives of the taxa present he inferred a warm temperate climate with a mean annual temperature of about 15° C, and a mean annual range of temperature of about 16° C. Based on analyses of megafossil floras from the Powder River Basin of Montana and Wyoming, Wolfe and Upchurch (1987) concluded that temperature and precipitation increased through the Tiffanian and Clarkforkian, and Wolfe (pers. comm.) suggests a mean annual temperature of about 17–18° C and a mean annual range of temperature of about 10° C during the latest Tiffanian. All of the figures from the Paleocene are broadly consistent with the mean annual temperature in temperate areas of eastern North America today and are also consistent with extrapolations based on the present climatic tol-

erances of the nearest living relatives of taxa such as *Cyclocarya, Ginkgo, Nordenskioldia,* and *Nyssidium.*

The floristic similarities between Paleocene floras and the composition of mixed mesophytic forest have led to the suggestion that this Recent vegetation type developed directly from an Early Tertiary "Arcto-Tertiary Geoflora" "with only minor changes in composition" (Chaney in Chaney & Axelrod, 1959, p. 12). It is now understood that plant communities are better viewed as complex mixtures of individual species with differing dispersal capabilities and ecological tolerances, and thus the "geoflora" concept oversimplifies the complexities involved in tracing vegetational and plant community change through geological time (see also Tiffney, 1985). Not only are Paleocene plant assemblages depauperate compared to Recent mixed mesophytic forest (Wolfe, 1966), but they also include a large proportion of taxa that are extinct. Of the Almont plants for which detailed information is available, *Nordenskioldia, Nyssidium, Palaeocarpinus, Parataxodium, Porosia,* and "*Viburnum*" are clearly extinct, while *Ginkgo, Cyclocarya, Cornus,* and *Meliosma,* as far as they are known, fall within the circumscription of extant genera. Nevertheless, the nearest living relatives of many extinct Paleocene plants are still associated in Recent mixed mesophytic forest and this suggests that the climatic and, perhaps, edaphic tolerances of some individual angiosperm lineages have either remained more or less constant, or have exhibited similar patterns of change over the last 60 million years. Future studies to document the relationships of other Paleocene plants, and to assess the extent to which these different angiosperm lineages have remained associated through time, will be of considerable importance to understanding the long-term development of extant plant families and Recent plant communities.

Acknowledgments

Literature Cited

ARNOLD, C. A., AND J. S. LOWTHER. 1955. A new Cretaceous conifer from northern Alaska. American Journal of Botany, **42**: 522–528.

BAILEY, I. W., AND C. G. NAST. 1945. Morphology and relationships of *Trochodendron* and *Tetracentron,* I. Stem, root and leaf. Journal of the Arnold Arboretum, **26**: 143–154.

BASINGER, J. F. 1981. The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. Canadian Journal of Botany, **59**: 2379–2410.

———. 1984. Seed cones of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. Canadian Journal of Botany, **62**: 281–289.

BASINGER, J. F., AND D. L. DILCHER. 1983. Fruits of *Cercidiphyllum* from the early Tertiary of Ellesmere Island, Arctic Canada. American Journal of Botany, **70**(5 part 2): 67 [Abstract.]

BELL, W. E. 1949. Uppermost Cretaceous and Paleocene floras of western Alberta. Geological Survey of Canada, Bulletin, **13**: 1–231.

BERRY, E. W. 1935. A preliminary contribution to the floras of the Whitemud and Ravenscrag Formations. Geological Survey of Canada, Memoir, **182**: 1–107.

BLUEMLE, J. P. 1983. Geologic and bedrock map of North Dakota. North Dakota Geological Survey, Miscellaneous Map, 25.

BONES, T. J. 1979. Atlas of fossil fruits and seeds from north central Oregon. Oregon Museum of Science and Industry, Occasional Papers in Natural Science, **1**: 1–23.

BROWN, R. W. 1939. Fossil leaves, fruits and seeds of *Cercidiphyllum.* Journal of Paleontology, **13**: 485–499.

———. 1962. Paleocene flora of the Rocky Mountains and Great Plains. USGS Professional Paper, **375**: 1–119.

CHANDLER, M. E. J. 1961. The Lower Tertiary Floras of Southern England, I. Palaeocene Floras: London Clay Flora (Supplement) and Atlas. British Museum (Natural History), London, xi + 354 pp., 34 pls.

———. 1964. The Lower Tertiary Floras of Southern England, IV. A Summary and Survey of Findings in the Light of Recent Botanical Observations. British Museum (Natural History), London, xii + 151 pp., 4 pls.

CHANDRASEKHARAM, A. 1974. Megafossil flora from the Genesee locality, Alberta, Canada. Palaeontographica, Abteilung B, Paläophytologie, 147: 1–41.

CHANEY, R. W. 1927. Geology and paleontology of the Crooked River Basin with special reference to the Bridge Creek flora. Carnegie Institution of Washington Publication, Contributions to Paleontology, 346: 45–138.

———. 1951. A revision of fossil Sequoia and Taxodium in western North America based on the recent discovery of Metasequoia. Transactions of the American Philosophical Society, 40: 169–263.

CHANEY, R. W., AND D. I. AXELROD. 1959. Miocene floras of the Columbia Plateau. Carnegie Institution of Washington Publication, Contributions in Paleontology, 617: 1–237.

CHU, K. L., AND W. S. COOPER. 1950. An ecological reconnaissance in the native home of Metasequoia glyptostroboides. Ecology, 31: 260–278.

COLLINSON, M. E. 1982. A preliminary report on the Senckenberg Museum Collection of fruits and seeds from Messel bei Darmstadt. Courier Forschungsinstitut Senckenberg, 56: 49–57.

———. 1983. Fossil Plants of the London Clay. Palaeontological Association, London, 121 pp.

———. 1984. Early Tertiary Hamamelidae: A contribution from isolated fossil organs. American Journal of Botany, 71(5 part 2): 109 [Abstract.]

———. 1986. The Felpham Flora:—A preliminary report. Tertiary Research, 8: 29–32.

COLLINSON, M. E., AND J. J. HOOKER. 1987. Vegetational and mammalian faunal changes in the Early Tertiary of southern England, pp. 259–304. In Friis, E. M., W. G. Chaloner, and P. R. Crane, eds., The Origins of Angiosperms and their Biological Consequences. Cambridge University Press, Cambridge.

CRANE, P. R. 1978. Angiosperm leaves from the Lower Tertiary of southern England. Courier Forschungsinstitut Senckenberg, 30: 126–132.

———. 1981a. Studies on the Flora of the Reading Beds (Upper Palaeocene). Ph.D. thesis, University of Reading.

———. 1981b. Betulaceous leaves and fruits from the British Upper Palaeocene. Botanical Journal of the Linnean Society, 83: 103–136.

———. 1984. A re-evaluation of Cercidiphyllum-like plant fossils from the British early Tertiary. Botanical Journal of the Linnean Society, 89: 199–230.

———. 1987. Vegetational consequences of the angiosperm diversification, pp. 107–144. In Friis, E. M., W. G. Chaloner, and P. R. Crane, eds., The Origins of Angiosperms and their Biological Consequences. Cambridge University Press, Cambridge.

———. 1989. Paleobotanical evidence on the early radiation of nonmagnoliid dicotyledons. Plant Systematics and Evolution, 162: 165–191.

CRANE, P. R., E. M. FRIIS, AND K. R. PEDERSEN. 1986. Angiosperm flowers from the Lower Cretaceous: Fossil evidence on early radiation of dicotyledons. Science, 232: 852–854.

CRANE, P. R., AND S. R. MANCHESTER. 1982. An extinct juglandaceous fruit from the Upper Palaeocene of southern England. Botanical Journal of the Linnean Society, 85: 89–101.

CRANE, P. R., S. R. MANCHESTER, AND D. L. DILCHER. 1988. The morphology and phylogenetic significance of Platanites hebridicus Forbes (Magnoliophyta) from the Palaeocene of Scotland. Palaeontology, 31: 503–517.

CRANE, P. R., AND R. A. STOCKEY. 1985. Growth and reproductive biology of Joffrea speirsii gen. et sp. nov., a Cercidiphyllum-like plant from the late Paleocene of Alberta, Canada. Canadian Journal of Botany, 63: 340–364.

———. 1986. Morphology and development of pistillate inflorescences in extant and fossil Cercidiphyllaceae. Annals of the Missouri Botanical Garden, 73: 382–393.

———. 1987. Betula leaves and reproductive structures from the Middle Eocene of British Columbia, Canada. Canadian Journal of Botany, 65: 2490–2500.

CREPET, W. L. 1984. Advanced (constant) insect pollination mechanisms: Pattern of evolution and implications vis-à-vis angiosperm diversity. Annals of the Missouri Botanical Garden, 71: 607–630.

CREPET, W. L., AND C. P. DAGHLIAN. 1981. Lower Eocene and Paleocene Gentianaceae: Floral and palynological evidence. Science, 214: 75–76.

CREPET, W. L., D. L. DILCHER, AND F. POTTER. 1975. Investigations of angiosperms from the Eocene of North America: A catkin with juglandaceous affinities. American Journal of Botany, 62: 813–823.

CREPET, W. L., AND E. M. FRIIS. 1987. The evolution of insect pollination in angiosperms, pp. 181–201. In Friis, E. M., W. G. Chaloner, and P. R. Crane, eds., The Origins of Angiosperms and their Biological Consequences. Cambridge University Press, Cambridge.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia University Press, New York, 1262 pp.

DILCHER, D. L. 1973. A paleoclimatic interpretation of Eocene floras of south-eastern North America, pp. 39–59. In Graham, A., ed., Vegetation and Vegetational History of Northern Latin America. Elsevier, Amsterdam.

DILCHER, D. L., AND S. R. MANCHESTER. 1986. Investigations of angiosperms from the Eocene of North America: Leaves of the Engelhardieae (Juglandaceae). Botanical Gazette, 147: 189–199.

DILCHER, D. L., F. POTTER, AND W. L. CREPET. 1976. Investigations of angiosperms from the Eocene of North America: Juglandaceous winged fruits. American Journal of Botany, 63: 532–544.

DOLPH, G. E., AND D. L. DILCHER. 1979. Foliar physiognomy as an aid in determining paleoclimate. Pa-

laeontographica, Abteilung B, Paläophytologie, **170:** 151–172.

ECKENWALDER, J. E. 1976. Comments on "A new classification of the conifers". Taxon, **25:** 337–339.

ENDRESS, P. K. 1986. Floral structure, systematics, and phylogeny in Trochodendrales. Annals of the Missouri Botanical Garden, **73:** 297–324.

———. 1987. Aspects of the evolutionary differentiation of the Hamamelidaceae and the Lower Hamamelididae. Plant Systematics and Evolution, **162:** 193–211.

EYDE, R. H. 1988. Comprehending *Cornus*: Puzzles and progress in the systematics of the dogwoods. Botanical Review, **54:** 233–351.

FLORIN, R. 1936. I. Die fossilen Ginkgophyten von Franz Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters, and I. Allgemeiner Teil. Palaeontographica, Abteilung B, Paläophytologie, **82:** 1–72.

FORBES, E. 1851. Note on the fossil leaves represented in plates II, III, IV. Quarterly Journal Geological Society of London, **7:** 103.

FRIEDRICH, W. L., AND L. A. SIMONARSON. 1982. *Acer*-funde aus dem Neogen von Island und Ihre Stratigraphische Stellung. Palaeontographica, Abteilung B, Paläophytologie, **182:** 151–166.

FRIIS, E. M. 1985. Structure and function in Late Cretaceous angiosperm flowers. Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter, **25:** 1–37.

FRIIS, E. M., P. R. CRANE, AND K. R. PEDERSEN. 1988. Reproductive structures of Cretaceous Platanaceae. Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter, **31:** 1–55.

FRIIS, E. M., AND W. L. CREPET. 1987. Time of appearance of floral features, pp. 155–179. *In* Friis, E. M., W. G. Chaloner, and P. R. Crane, eds., The Origins of Angiosperms and their Biological Consequences. Cambridge University Press, Cambridge.

GARDNER, J. S. 1887. On the leaf beds and gravels of Ardtun, Carsaig, etc., in Mull. Quarterly Journal Geological Society of London, **43:** 270–300.

GREGOR, H. J. 1982. Die Jungtertiären Floren Süddeutschlands. Enke, Stuttgart. 278 pp.

HARR, J. L., AND F. T. C. TING. 1976. Modern and Paleocene *Metasequoias*: A comparison of foliage morphology, pp. 181–201. *In* Romans, R. C., ed., Geobotany. Plenum, New York.

HARRIS, T. M., W. MILLINGTON, AND J. MILLER. 1974. The Yorkshire Jurassic flora. IV. Ginkgoales, Czekanowskiales. British Museum (Natural History), London, viii + 150 pp., 8 pls.

HEER, O. 1869. Contributions to the fossil flora of the North Greenland being a description of the plants collected by Mr. Edward Whymper during the summer of 1867. Philosophical Transactions of the Royal Society of London, **159**(2): 445–488. [Reprinted as Flora Fossilis Arctica, 2(4), 1871.]

———. 1870. Die Miocene Flora und Fauna Spitzbergens. Konglica Svenska Vetenskapsakademiens Handlingar 8(7): 1–98. [Reprinted as Flora Fossilis Arctica, 2(3), 1871.]

HICKEY, L. J. 1977. Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota. Geological Society of America Memoir, **150:** 1–181.

———. 1980. Paleocene stratigraphy and flora of the Clarks Fork Basin. University of Michigan Papers on Paleontology, **24:** 33–49.

HOLLICK, A. 1936. The Tertiary floras of Alaska. USGS Professional Paper, **182:** 1–185.

HOLTZMAN, R. C. 1978. Late Paleocene mammals of the Tongue River Formation, western North Dakota. North Dakota Geological Survey, Report of Investigation, **65:** 1–88.

ILJINSKAJA, J. 1953. Monograph of the genus *Pterocarya* Kunth [in Russian]. Trudy Botanicheskogo Instituta Akademii Nauk SSSR, Ser. 1, Flora i sistematika vyshikh rastenii, **10:** 7–123.

———. 1974. *Trochodendroides* Berry, *Nyssidium* Heer, pp. 115–124. *In* Takhtajan, A., ed., Magnoliophyta Fossilia URSS, I, Magnoliaceae–Eucommiaceae. Nauka, Leningrad.

JARZEN, D. M., AND G. NORRIS. 1975. Evolutionary significance and botanical relationships of Cretaceous angiosperm pollen in the western Canadian interior. Geoscience and Man, **11:** 47–60.

JOHNSON, T. 1937. Notes on the Tertiary flora of Scotland. Transactions and Proceedings of the Botanical Society of Edinburgh, **32:** 291–340.

KNOBLOCH, E., AND D. H. MAI. 1984. Neue Gattungen nach Früchten und Samen aus dem Cenoman bis Maastricht (Kreide) von Mitteleuropa. Feddes Repertorium, **95:** 3–41.

———. 1986. Monographie der Früchte und Samen in der Kreide von Mitteleuropa. Rozpravy Ústredniko Ústavu Geologickéno Praha, **47:** 1–219.

KNOWLTON, F. H. 1930. The flora of the Denver and associated formations of Colorado. USGS Professional Paper, **155:** 1–142.

KOCH, B. E. 1963. Fossil plants from the Lower Paleocene of the Agatdalen (Angmartussut) Area, Central Nugssuaq Peninsula, North-west Greenland. Meddelelser om Grønland, **172:** 1–120.

———. 1978. Some fossil angiospermous fruits from the Danian of West Greenland. Courier Forschungsinstitut Senckenberg, **30:** 47–53.

KRASSILOV, V. A. 1973a. Mesozoic plants and the problem of angiosperm ancestry. Lethaia, **6:** 163–178.

———. 1973b. Cuticular structure of Cretaceous angiosperms from the Far East of the USSR. Palaeontographica, Abeilung B, Paläophytologie, **142:** 105–116.

———. 1976. The Tsagayan Flora of Amur Region [in Russian]. Nauka, Moscow, 92 pp., 43 pls.

———. 1977. The origin of angiosperms. Botanical Review, **43:** 143–176.

———. 1978. Late Cretaceous gymnosperms from Sakhalin, USSR, and the terminal Cretaceous event. Palaeontology, **21:** 893–905.

KRYSHTOFOVICH, A. N. 1956. Oligocene Flora of Mount Ashutus in Kazakstan [in Russian]. Paleobotanica Fasciculus I. Institutum Botanicum Nomine V. L. Ko-

marovii Academiae Scientarium URSS. ACTA Series VIII. Moscow, 179 pp. + 61 pls.

————. 1958. The Cretaceous flora of Anadyrland [in Russian], pp. 9–70. *In* Takhtajan, A., ed., Paleobotanica Fasciculus III. ACTA Series VIII. Moscow.

Kvaček, Z. 1971. A new *Platanus* from the Bohemian Tertiary. Paläontologische Abhandlungen B Paläophytologie, 3(4): 435–439.

Laurent, L. 1912. Flore fossile des schistes de Menat (Puy-de-Dôme). Annales du Musée d'Histoire Naturelle de Marseille, 14: 1–246.

Lerud, J. 1982. Lexicon of stratigraphic names of North Dakota. North Dakota Geological Survey, Report of Investigation, 71: 1–139.

Lesquereux, L. 1878. Contributions to the flora of the Western Territories. II. The Tertiary flora. Report of the USGS Geological Survey of the Territories, 7: 1–366.

MacGinitie, H. D. 1953. Fossil plants of the Florissant Beds, Colorado. Carnegie Institution of Washington Publication, 599: 1–198.

Mai, D. H. 1980. Zur Bedeutung von Relikten in der Florengeschichte, pp. 281–301. *In* 100 Jahre Arboretum (1877–1979). Berlin.

————. 1981. Entwicklung und klimatische Differenzierung der Laubwaldflora Mitteleuropas in Tertiär. Flora, 171: 525–582.

————. 1987. Neue Früchte und Samen aus paläozänen Ablagerungen Mitteleuropas. Feddes Repertorium, 98: 197–229.

Mai, D. H., and H. Walther. 1985. Die Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR). Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden, 28: 1–200.

Manchester, S. R. 1986. Vegetative and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of western North America. Botanical Gazette, 147: 200–226.

————. 1987. The fossil history of the Juglandaceae. Monographs in Systematic Botany from the Missouri Botanical Garden, 21: 1–137.

————. 1988. Fruits and seeds of *Tapiscia* (Staphyleaceae) from the Middle Eocene of Oregon, USA. Tertiary Research, 9: 59–66.

Manchester, S. R., and P. R. Crane. 1987. A new genus of Betulaceae from the Oligocene of western North America. Botanical Gazette, 148: 263–273.

Manchester, S. R., and D. L. Dilcher. 1982. Pterocaryoid fruits (Juglandaceae) in the Paleogene of North America and their evolutionary and biogeographic significance. American Journal of Botany, 69: 275–286.

Manum, S. 1962. Studies in the Tertiary flora of Spitzbergen, with notes on Tertiary floras of Ellesmere Island, Greenland and Iceland, Norsk Polarinstitutt Skrifter, 125: 1–127.

————. 1966. *Ginkgo spitzbergensis* n. sp. from the Palaeocene of Spitzbergen and a discussion of certain Tertiary species of *Ginkgo* from Europe and North America. Norsk Polarinstitutt Arbok, 1965: 49–58.

Mastroguiseppe, J. D., A. A. Cridland, and T. P.

Bogyo. 1970. Multivariate comparison of fossil and Recent *Ginkgo* wood. Lethaia, 3: 271–277.

Mathiesen, F. R. 1932. Notes on some fossil plants from East Greenland. Meddelelser om Grønland, 85(4): 1–63.

Miki, A. 1977. Late Cretaceous pollen and spore floras of northern Japan: Composition and interpretation. Journal of the Faculty of Science, Hokkaido University Series IV. Geology and Mineralogy, 17: 399–436.

Muller, J. 1981. Fossil pollen records of extant angiosperms. Botanical Review, 47: 1–142.

Nast, C. G., and I. W. Bailey. 1945. Morphology and relationships of *Trochodendron* and *Tetracentron,* II. Inflorescence flower and fruit. Journal of the Arnold Arboretum, 26: 267–276.

Prynada, V. D. 1962. Flore Mésozoique de Siberie Orientale et de Transabaikalie [in Russian]. Moscow, 368 pp., 25 pls.

Reid, E. M., and M. E. J. Chandler. 1933. The London Clay Flora. British Museum (Natural History), London, viii + 561 pp., 35 pls.

Rothwell, G. W., and J. F. Basinger. 1979. *Metasequoia milleri* n. sp., anatomically preserved pollen cones from the Middle Eocene (Allenby Formation) of British Columbia. Canadian Journal of Botany, 57: 958–970.

Saporta, G. D. 1868. Prodome d'une flore fossile des travertins anciens de Sézanne. Mémoires de la Société Géologique de France, sér. 2, 8: 289–436.

Schloemer-Jäger, A. 1958. Altertiäre pflanzen aus flözen der Brögger-Halbinsel Spitzbergens. Palaeontographica, Abteilung B, Paläophytologie, 104: 39–103.

Schweitzer, H. J. 1974. Die Tertiären Koniferen Spitzbergens. Palaeontographica, Abteilung B, Paläophytologie, 149: 1–89.

Scott, R. A. 1954. Fossil fruits and seeds from the Eocene Clarno Formation of Oregon. Palaeontographica, Abteilung B, Paläophytologie, 96: 66–97.

Scott, R. A., and E. A. Wheeler. 1982. Fossil woods from the Eocene Clarno Formation of Oregon. International Association of Wood Anatomists Bulletin, 3: 135–148.

Seward, A. C. 1939. The Western Isles through the mists of ages. Report of the British Association for the Advancement of Science, 1: 11–29.

Seward, A. C., and W. N. Edwards. 1941. Fossil plants from East Greenland. Annals and Magazine of Natural History, 11(8): 169–176.

Seward, A. C., and R. E. Holltum. 1924. Tertiary plants from Mull, pp. 67–90. *In* Bailey, E. B., C. T. Clough, W. B. Wright, J. E. Richey, and G. V. Wilson, eds., Tertiary and Post Tertiary Geology of Mull, Loch Aline and Oban. Memoirs of the Geological Survey of Scotland. HMSO, Edinburgh.

Smith, A. C. 1945. A taxonomic review of *Trochodendron* and *Tetracentron*. Journal of the Arnold Arboretum, 26: 123–141.

Spicer, R. A., and A. G. Greer. 1986. Plant taphonomy in fluvial and lacustrine systems, pp. 10–26. *In* Gastaldo, R. A., ed., Land Plants Notes for a Short

Course. Department of Geological Sciences Studies in Geology 15, University of Tennessee, Knoxville.

SPICER, R. A., AND C. R. HILL. 1979. Principal components and correspondence analyses of quantitative data from a Jurassic plant bed. Review of Palaeobotany and Palynology, 28: 273–299.

SPONGBERG, S. A. 1979. Cercidiphyllaceae hardy in temperate North America. Journal of the Arnold Arboretum, 60: 367–376.

STOCKEY, R. A., AND P. R. CRANE. 1983. *In situ Cercidiphyllum*-like seedlings from the Paleocene of Alberta, Canada. American Journal of Botany, 70: 1564–1568.

STOCKEY, R. A., AND S. R. MANCHESTER. 1988. A fossil flower with *in situ Pistillipollenites* from the Eocene of British Columbia. Canadian Journal of Botany, 66: 313–318.

SWAMY, B. G. L., AND I. W. BAILEY. 1949. The morphology and relationships of *Cercidiphyllum*. Journal of the Arnold Arboretum, 30: 187–210.

SZAFEROWA, J. J. 1958. The genus *Carpinus* in Europe in the paleobotanical literature. Monographie Botanicae, 7: 1–59.

TAKAHASHI, K. 1974. Palynology of the Upper Aptian Tanohata Formation of the Miyako Group, northeast Japan. Pollen Spores, 16: 535–564.

TAKHTAJAN, A. 1974. Magnoliophyta Fossilia URSS [in Russian]. Nauka, Leningrad, 188 pp., 124 pls.

TANAI, T. 1972. Tertiary history of vegetation in Japan, pp. 235–255. *In* Graham, A., ed., Floristics and Paleofloristics of Asia and Eastern North America. Elsevier, Amsterdam.

———. 1981. The revision of the so-called "*Cercidiphyllum*" leaves from the Paleogene of North Japan. Journal of the Faculty of Science, Hokkaido University Series IV. Geology and Mineralogy, 19: 451–484.

———. 1983. Revisions of Tertiary *Acer* from East Asia. Journal of the Faculty of Science, Hokkaido University Series IV. Geology and Mineralogy, 20: 291–390.

THANIKAIMONI, G. 1984. Menispermacées: Palynologie et systematique. Institut Français de Pondichéry, Travaux de la Section Scientifique et Technique, 18: 1–135.

TIFFNEY, B. H. 1984. Seed size, dispersal syndromes, and the rise of the angiosperms: Evidence and hypothesis. Annals of the Missouri Botanical Garden, 71: 551–576.

———. 1985. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. Journal of the Arnold Arboretum, 66: 73–94.

TRALAU, H. 1968. Evolutionary trends in the genus *Ginkgo*. Lethaia, 1: 63–101.

UPCHURCH, G. R., AND J. A. WOLFE. 1987. Mid-Cretaceous to Early Tertiary vegetation and climate: Evidence from fossil leaves and woods, pp. 75–105. *In*

Friis, E. M., W. G. Chaloner, and P. R. Crane, eds., The Origins of Angiosperms and their Biological Consequences. Cambridge University Press, Cambridge.

VAN BEUSEKOM, C. F. 1971. Revision of *Meliosma* (Sabiaceae) section *Lorenzanea* excepted, living and fossil, geography and phylogeny. Blumea, 19: 355–529.

WALTHER, H. 1972. Studien über tertiäre *Acer* Mitteleuropas. Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden, 19: 1–309.

WANG, C. W. 1961. The Forests of China. Maria Moors Cabot Foundation, Harvard University, Publication 5, xiv + 313 pp.

WARD, L. F. 1887. Types of the Laramie Flora. USGS Bulletin, 37: 1–117.

WEST, R. M., M. R. DAWSON, L. J. HICKEY, AND A. D. MIALL. 1981. Late Cretaceous and Paleogene sedimentary rocks, eastern Canadian Arctic and related North Atlantic areas. *In* Kerr, J. W., and A. J. Ferguson, eds., Geology of the North Atlantic Borderlands, Canadian Society of Petroleum Geologists, Memoir, 7: 279–298.

WILLIS, J. C. 1973. A Dictionary of Flowering Plants and Ferns. Cambridge University Press, Cambridge, lxvi + 1245 pp.

WING, S. L., AND B. H. TIFFNEY. 1987a. Interactions of angiosperms and herbivorous tetrapods through time, pp. 203–224. *In* Friis, E. M., W. G. Chaloner, and P. R. Crane, eds., The Origins of Angiosperms and their Biological Consequences. Cambridge University Press, Cambridge.

———. 1987b. The reciprocal interaction of angiosperm evolution and tetrapod herbivory. Review of Palaeobotany and Palynology, 50: 179–210.

WOLFE, J. A. 1966. Tertiary plants from the Cook Inlet Region, Alaska. USGS Professional Paper, 398B: 1–32.

———. 1973. Fossil forms of Amentiferae. Brittonia, 25: 334–355.

———. 1977. Paleogene floras from the Gulf of Alaska Region. USGS Professional Paper, 997: 1–108.

———. 1979. Temperature parameters of humid to mesic forests of Eastern Asia, and relation to forests of other regions of the Northern Hemisphere and Australasia. USGS Professional Paper, 1106: 1–37.

WOLFE, J. A., AND T. TANAI. 1987. Systematics, phylogeny, and distribution of *Acer* (Maples) in the Cenozoic of western North America. Journal of the Faculty of Science, Hokkaido University Series IV. Geology and Mineralogy, 22: 1–246.

WOLFE, J. A., AND G. R. UPCHURCH. 1986. Vegetation, climatic and floral changes at the Cretaceous–Tertiary boundary. Nature, 324: 148–152.

———. 1987. Maestrichtian–Paleocene vegetation and climate of the Powder River Basin, Wyoming and Montana. Geological Society of America Abstracts, 1987: 896.